The post-embryonic ontogeny of *Acridomorpha*
(Orthoptera)

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Preface.

Accumulating the material necessary for a study of the earlier stages of *Acridomorpha* presented numerous difficulties. It was not always possible to obtain living material for rearing in the laboratory, and some of the species are highly specialised in their food requirements. Material already collected and preserved, sometimes abundant, must be treated with great caution, owing to the possibility of misidentification. These circumstances limited the scope of the work presented in this paper.

It was considered at the outset that this research would be a comparatively simple task, but in the course of it more problems arose than were solved.

Acknowledgements.

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INTRODUCTION.

There is a disagreement regarding the naming of the post-embryonic stages of insects. The main controversy is in the use of the terms *larva* and *nymph.*

In various countries and languages, the usage of these terms is traditional and has lost its logical and scientific implication. It was apprehended by entomologists long ago and has been discussed in a number of scientific papers (*see* China *et al.,* 1958). However, the terminology has still not been rigidly fixed and is used differently by various authors.

In some cases it is not possible to draw a line between the definitions of larva and nymph, but in many cases it is straightforward. It is not proposed here to discuss the whole problem, since we are concerned in this paper with the suborder *Acridomorpha* only, for which it suffices to adopt the opinion that the term *nymph* should be used for the Exopterygota which lack a pupal stage, the term *larva* being reserved for the Endopterygota which possess a pupal stage. In the light of this definition, all juvenile stages in *Acridomorpha* are nymphs. The whole period, from hatching to the final moult, is here considered, in agreement with the views of many other authors, as the nymphal stage or period, which is determinable by external morphological features; internal characters, for example genitalia, are not considered as features suitable for the definition of nymphal stages because they continue to develop during the life of the imago and attain final development at sexual maturity.

The nymphal stage is divided into several sub-stages called instars or stadia, separated by moults or ecdyses.

There is a difficulty concerning the term to be used for the very brief sub-stage which in *Acridomorpha* immediately follows hatching and is terminated by the first moult. Many authors have applied the term "larva" to the insect during this period, the general body-form being then more embryonic than nymphal and quite different from that of all subsequent sub-stages; as recently as 1966 Uvarov, in his work *Grasshoppers and Locusts,* has retained the term "vermiform larva" for it. This first sub-stage is undoubtedly the true first instar, as Uvarov points out, but since the term "first instar" has for many years been generally applied to the next sub-stage, serious confusion would arise if it were now applied to the first. In the present work, therefore, the author, while disliking the terminological inaccuracy involved, feels compelled to continue the practice of using "vermiform larva" for the true first instar, and "first instar" for the true second.

Only the morphological aspect of the nymphal development was studied; other aspects such as coloration, physiology and ethology are omitted as only fragmentary data are available in these respects.

CLASSIFICATION.

The system adopted in this paper is, like every system in taxonomy, a temporary one, based mostly on external morphological characters and the phallic complex. As more data are accumulated more changes will be made, with more possibilities for an approach towards the phylogenetic system which could be proved and used as the true basis for classification. The present arrangement follows the system of Dirsh 1966. It is essential to outline the system here for the understanding of the systematic position of the nymphs.

It is outside the scope of this work to discuss the position and interrelation of *Acridomorpha* in the group of Orthopteroid insects; only the system within the group is considered, but some phylogenetic aspects are discussed below.

The group of insects which was formerly called *Acridoidea* is considered here as the suborder *Acridomorpha* and is subdivided as follows:

Order ORTHOPTERA.

Suborder ACRIDOMORPHA.

Paurometabolous insects. Primarily winged. Mandibulate. Antenna 7-33 segmented. Cerci unsegmented. Styli absent. Ovipositor short, six-valved, visual part four-valved. Phallic complex consists of ectophallus, endophallus and epiphallus. All tarsi three-segmented.

Superfamily **EUMASTACOIDEA.**

Penis primarily formed by a single sclerite. Tympanal organ absent. Stridulatory mechanism absent.
Families: **Eumastacidae, Proscopiidae.**

Superfamily TRIGONOPTERYGOIDEA.

Phallic complex in reversed position. Penis formed by two paired sclerites. Cingulum present. Stridulatory mechanism absent. Tympanal organ absent.
Family: **Trigonopterygidae.**

Superfamily PNEUMOROIDEA.

Cingulum of phallic complex and penis poorly developed or absent. Epiphallus shield-like. Abdomino-femoral stridulatory mechanism (third tergite and inner side of hind femur) present. Tympanal organ absent.
Families: **Tanaoceridae, Xyronotidae, Pneumoridae.**

Superfamily ACRIDOIDEA.

Cingulum of phallic complex present. Penis formed by two paired sclerites. Stridulatory mechanism of various types present or absent. Tympanal organ primarily present.

Families: **Charilaidae, Pamphagidae, Pyrgomorphidae, Ommexechidae, Lathiceridae, Lentulidae, Pauliniidae, Acrididae.**

EGGS.

The post-embryonic development begins when the insect emerges from the egg. However, a short note concerning the egg is necessary.

In all *Acridomorpha* the eggs are roughly elongate-cylindrical and in most cases slightly curved, like banana fruit. Both ends are rounded or obtusely conical. In elongate, narrow species, the eggs are themselves narrower and more elongate than in the short sturdy species.

NYMPHAL DEVELOPMENT.

The most drastic morphological change occurs during the transformation from the vermiform larva to the first instar. The second greatest change occurs during the last ecdysis, when the nymph transforms into the imago, and in so doing acquires wings, in most species. The intermediate instars develop by a more gradual process.

The vermiform larva is covered by what has been called a provisional cuticle, which is chitinous, lacks cells and is virtually the same as the cuticle of subsequent nymphal instars. In some species studied this cuticle is sparsely covered with small bristles, which probably facilitate movement to the soil surface. It envelops the whole body, limbs and appendices.

The emergence from the egg-shell and the movement to the surface through the egg-pod and the soil are achieved by active movement of the insect and pulsation of the cervical ampulla. The vermiform larva performs wriggles in a manner which ultimately brings it to the surface. The limbs at this period do not take any active part; as far as was observed they are immobile during the whole of this period.

The life of the vermiform larva is very short. After emergence from the egg, the process of apolysis can already be noticed by simple observation of the insect under illumination and low magnification of the microscope, and after arrival at the surface of the soil, the process of ecdysis begins almost immediately. Within a few minutes of reaching the surface the primary cuticle splits along the ecdysial cleavage line on the dorso-frontal part of the head and the dorsum of the pronotum. This splitting is effected by the blood pressure of the cervical ampulla, which is a characteristic feature of the vermiform larva. The ampulla is a bladder-like inflation of the membrane on the dorsal side between head and pronotum. From this split the first-instar nymph emerges, sometimes leaving the whole "primary" cuticle intact, sometimes shedding the cuticle of the limbs separately and a little later.

The vermiform larva largely retains the embryonic appearance: the head is bent down, so that its axis coincides with the sagittal axis of the whole body and its position may be described as opistognathous; the antennae are folded down towards the posterior end along the head; the mandibles are straight and visible from the sides; the legs are folded at the joints and tightly appressed to the body; the epiproct, or supra-anal plate, if elongate, is bent down and towards the cephalic end of the body and is also appressed to it; and the cerci are bent inwards and downwards, parallel to the end of the abdomen. All these bends and positions of the appendices and limbs can be observed in the embryo before hatching. It is proposed here to call their position the "embryonic position". The embryonic position described usually disappears at the first moult, but in some appendages, for example the cerci, it may persist through the first instar and disappear only in the second. The cervical ampulla is strongly developed in the vermiform larva and disappears in the first instar.

Growth and differentiation, which proceed throughout the whole nymphal stage, find their expression in increasing body size and morphological changes of external and internal organs. Changes in the internal organs, such as the development of the endoskeleton muscles and genital organs, occur in the nymphal stage, but knowledge of them is extremely scanty. Also very little is known of the concomitant physiological changes.

In *Acridomorpha* growth and differentiation are parallel and inseparable processes, but are subjected to a certain rhythm. The growth process manifests itself mostly during the inter-instar periods, while differentiation is mostly in the pre- and post-ecdysis periods, culminating in ecdysis itself.

The process of differentiation in *Acridomorpha* is in general progressive, but there are several cases of organs which are more developed in the nymphs, being reduced or even lost in the imago. For example: the supra-anal plate is strongly elongate in all the nymphal instars in *Acrida, Truxalis, Mesopsis* and some other genera, but is sharply decreased in length at the final ecdysis (fig. 22); and the glassy tubercles on the lateral lobes of the pronotum in *Gastrimargus* (fig. 47) and *Humbe* (fig. 48) are strongly developed in the first instar, but gradually decrease in the subsequent instars to disappear completely in the third. These characters are regressive, in the latter case to the point of complete disappearance.

Number of nymphal instars.

There are numerous data scattered in many papers concerning the number of nymphal instars in *Acridomorpha*. Unfortunately not all of them are reliable. Below (Table 1) 40 reasonably reliable cases have been selected for the purpose of estimating the number of instars.

In 19 of the 40 species males and females have the same number of instars; in 21 species females have one or two more instars than males.

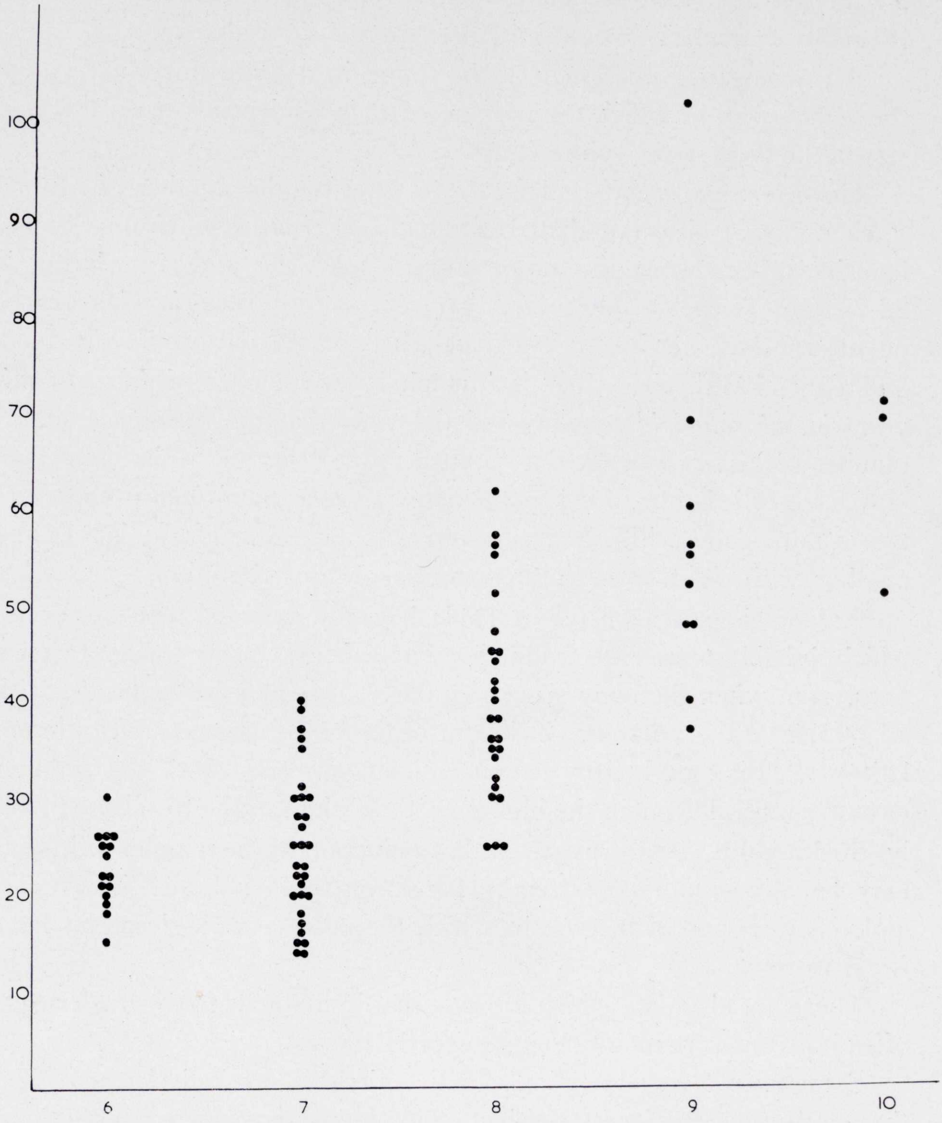


Fig. 1.—Scatter diagram. Ordinate: length of body; abscissa: number of instars (including vermiform larva).

On analysing the species listed in Table 1 it becomes apparent that in those in which the females have more instars, the females are much larger than the males. When the data are plotted as a scatter diagram (fig. 1) it is clearly indicated that the number of instars is a function of the final length of the body. The longer insects have more instars than the shorter ones. There are, however, exceptions: certain small insects, like *Chrotogonus robertsi,* may have 5-6 instars in males and 5-7 in females (Latif & Haq, 1951). This latter number of instars is usually characteristic of much larger species of Acridids.

An analogous situation is to be found in a quite unrelated group, the *Arachnida,* in which the number of ecdyses depends upon the final size of the body of the spider (Savory, 1964).

However, many different factors may affect the number of instars. Parker (1930) observed that *Melanoplus mexicanus mexicanus* Sauss. has five instars when the temperature is 32-37° C. and six when it is 22-27° C. Telenga (1930) noted that *Schistocerca gregaria* when reared on lucerne has one instar less than when reared on gramineous food, and Key (1936), observing the nymphal development of *Locusta migratoria migratorioides,* expressed the view that the difference in the number of instars may be due to an hereditary factor. Similarly Jago (1963) recorded that in *Eyprepocnemis plorans meridionalis* there are two strains, one with seven instars (after the vermiform larva) and another with eight, even in the same laboratory conditions.

Among the species listed in Table 1 it may be noted that the species which inhabit temperate countries have fewer instars than tropical ones, even when the body size is similar. This may be connected with adaptation to the difference in length of the breeding season at different latitudes. Photoperiodism also may be concerned, since the summer days are much longer in the higher latitudes than in the tropics. Finally, Borkhsenius (1963) suggested that reduction in the number of instars may be an evolutionary trend. He mentioned examples in Coccids and other groups of insects, in which the more advanced species have fewer instars.

There are also data which indicate that individuals from smaller eggs often have an extra moult (Wigglesworth, 1965).

Sometimes a particular individual undergoes one ecdysis more than the number normal for its species. These extra ecdyses are not accompanied by morphological changes and are a result of some nutritional deficiency or other unknown factor. In *Acridomorpha* they are considered as representing addititonal instar.

Considering the problem from every aspect, it seems that the number of instars is not a rigidly fixed feature of a species, but can fluctuate under the influence of various conditions; in some cases it may be genetically predetermined and possess an evolutionary trend towards reduction.

The moulting is caused by the so-called "moulting hormone" which appears to be non-specific (Wigglesworth, 1965). It is excreted by glands of ectodermal origin located in the lower part of the head (ventral glands) and in the anterior part of the thorax (prothoracic glands).

In Acridids the stimulation of the glands which produce secretion for triggering the moulting process is effected by a complicated neuro-endocrine system. The theory is advanced that in *Locusta* the production of the neurosecretory material is constant in the neurosecretory cells and that there is a constant release of it from the corpora cardiaca, but that impulses for production and release originate in the stretch receptors of the pharynx and are then conducted by nerves to the brain, from which they pass through the recurrent nerve and hypocerebral ganglion to the corpora cardiaca (Clarke & Langley, 1963).

TABLE 1.

Number of nymphal instars (after the vermiform larva)

Name of species	Males	Females	Author
Acrida bicolor	6	7-8	Hafez & Ibrahim, 1958
Acrotylus angulatus	5-6	5-6	Chesler, 1938
Aiolopus thalassinus	4	4	Bey-Bienko, 1928
Calliptamus italicus	5	6	Pichler, 1956
Cannula pellucida	5	5-6	Shotwell, 1941
Choroedocus capensis	6	7	Tinkham, 1940
Chrotogonus robertsi	5-6	5-7	Latif & Haq, 1951
Dissosteira carolina	5-6	5-6	Shotwell, 1941
Dociostaurus kraussi	4	5	Plotnikov, 1926
Dociostaurus maroccanus	5	5	Jannone, 1939
Epacromius tergestinus	4	4	Chesler, 1938
Euchorthippus pulvinatus	5	5	Dovnar-Zapolsky, 1926
Euthystira brachyptera	4	4	Bey-Bienko, 1928
Eyprepocnemis plorans meridionalis	6-8	6-8	Antoniou & Hunter-Jones, 1957; Jago, 1963
Eyprepocnemis roseus roseus	5	6	Katiyar, 1953
Eyprepocnemis hokutensis	6	7	Tinkham, 1940
Gastrimargus africanus	4-6	5-6	Hunter-Jones & Ward, 1960
Gastrimargus musicus	5	5	Common, 1948

Name of species	Males	Females	Author
Gastrimargus procerus	5	5	Dirsh, 1959
Gomphocerippus rufus	4	4	Bey-Bienko, 1928
Gomphocerus sibiricus	4	4	Ilenko, 1930
Hieroglyphus banian	6	7	Coleman & Kannan, 1911
Loboscelíana femoralis	7	7	Dirsh, 1958
Melanoplus differentialis	6	6	Shotwell, 1941
Neopodismopsis abdominalis	4	4	Griddle, 1930
Nomadacris septemfasciata	6-7	6-7	Burnett, 1951; Albrecht, 1955
Oedaleus nigrofasciatus	5	5	Chesler, 1938
Oedipoda coerulescens	4	4	Bey-Bienko, 1928
Ornithacris turbida	6	8	Uvarov, 1966
Oxyrrhepes cantonensis	6	7	Tinkham, 1940
Parahieroglyphus bilineatus	6	6	Katiyar, 1953
Parapleurus alliaceus	5	5	Dovnar-Zapolsky, 1926
Paracyptera microptera	5	5	Berezhkov, 1956
Poekilocerus hieroglyphicus	7	8	Uvarov, 1966
Psophus stridulus	4	4	Bey-Bienko, 1928
Pyrgomorpha kraussi	5	6-7	Uvarov, 1966
Schistocerca flavofasciata	5	6	Kevan, 1943
Schistocerca gregaria	5-6	5-6	Popov, 1965
Trilophidia conturbata	5	5	Chesler, 1938
Zonocerus elegans	5	6	Chesler, 1938

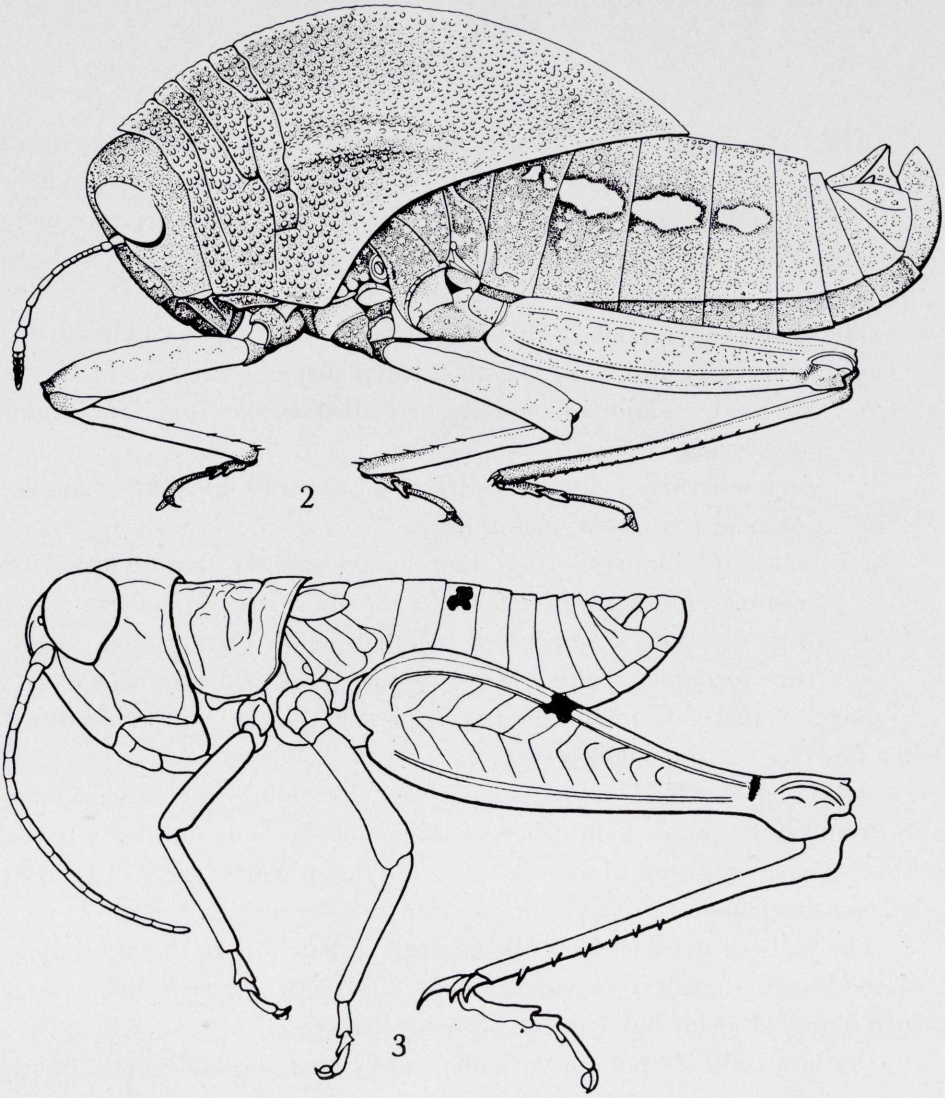
NYMPHS AND NEOTENY.

There is no definite proof that neoteny exists in *Acridomorpha,* but the opinion has been expressed that such a possibility should not be excluded.

Dirsh (1963) described three new genera *(Parabullacris, Pneumoracris* and *Paraphysemacris)* and species of *Pneumoridae* without the inflated body in the male (fig. 2) which is characteristic of the family in general, and with wings vestigial, hidden or absent and the abdominal-femoral stridulatory mechanism also vestigial or absent. All of them have fully developed internal genitalia in both sexes. In 1965 Dirsh, and previously Van Son *(in litt.),* expressed the opinion that these genera and species, being parallel to the already known genera with inflated male bodies, may be neotenic forms.

In 1958, Dirsh described a genus and species *Acocksacris karruensis* from Great Karroo (South Africa), with a very small body (male

8,2, female 9 mm.) and of a strangely nymphal appearance (fig. 3). It had not occurred to the author at that time that the species might be neotenic. Considering that the Great Karroo is an extremely arid area with poor, short-lived vegetation, it is possible that species in it have become adapted to the unfavourable conditions by developing neoteny.



Figs. 2-3.—2) *Parabullacris vansoni,* adult male. 3) *Acocksacris karruensis,* adult male. Possibly both neotenic.

In the family *Lentulidae* also, many species have a strikingly nymphal appearance in the imago stage which may be due to neoteny.

All these possibilities are purely hypothetical and are mentioned here in the hope of directing attention to the need for researches on them. They will be more accurately assessable when the early stages of these species are better known.

BODY.

The body shape of *Acridomorpha* nymphs in the first instar, in all groups, is rather uniform. In most groups the body is aprroximately cylindrical and in some, for example *Proscopiidae,* it is very narrowly so, this difference being connected with the final shape of the body in the imago.

The shape of the body of the imago can be classified as follows:

a. Cylindrical, this being the most usual shape.

b. Narrowly cylindrical, usually described as stick-like (for example, *Acrida, Truxalis).*

c. Very narrowly cylindrical, described as straw-like (for example, *Cannula, Proscopia, Mesopsis).*

d. Laterally compressed, so that height greater than width (for example, *Plagiotriptus,* some *Tropidauchen, Xyronotus).*

e. Dorso-ventrally compressed, so that width greater than height (for example, *Lathicerus, Trachypetrella, Batrachotetrix).*

Parts of the body follow their own patterns, which can be classified in a few types as the whole body can.

Attaining the final, adult, shape does not follow the same course in groups and species with different shapes of the body and body parts. Every genus or group of genera follows its own course, as will be seen later in this paper.

The body of nymphs from the moment of hatching to the attainment of the imago stage grows continuously. Growth proceeds throughout each nymphal instar but is greater during ecdysis.

Przibram (1922) put forward the theory that the body mass of insects doubles between one ecdysis and the next owing to cell division, each cell being divided and the number of cells doubled. The linear growth then increases $\sqrt{2} = 1{,}26$ times. These so-called Przibram's quotients in most cases do not agree with the facts in *Acridomorpha.*

The increase of length, volume and mass may in some cases be expressed as an exponential growth. This concept was propounded by Janisch (1927). There are, however, so many biological factors interfering with the pure exponential formula, that an application of it would be of doubtful value.

Gross (1964) expressed the opinion that the regulation of growth of organisms is determined by their functional demands. This is true for all the *Acridomorpha* studied.

Generally speaking, there are as many mathematical formulae and interpretations of the process of growth as there are authors who studied them. The opinion that a universal growth equation is a fiction (Medawar, 1945) can be fully endorsed for *Acridomorpha*. The formula most widely used is the Huxley (1924) formula of allometric growth: $Y = CX^k$.

It is not only the species that differ in the pattern of growth. Even the various populations of the same species (Davey, 1954) or individuals reared in different ecological conditions, including diet (Hodge, 1933), may differ in the pattern of increase in body size, and even in the number of instars (see p. 421).

In this paper growth is expressed graphically. For the purpose of estimating the total growth between the first instar and the imago, the formula of the specific productivity of growth is used (Schmalhausen, 1928):

$$U = \frac{\log X_2 - \log X_1}{0{,}4343}$$

Where U indicates the specific productivity of growth; X is the interval between the stages of development (instars or times) and can be used for mass, length, volume etc.; and 0,4343 is the coefficient for conversion of decimals to natural logarithms.

A very lucid study of the problem of growth was presented by A. E. Needham in 1964. However, the problem became so deeply involved with numerous biological aspects of the organisms that in the narrow field of the present investigation, only the most general points can be considered, as follows.

Mass of body (M). This is determined by weight. In this respect there are only two species with reliable data from the first instar to the adult.

In *Locusta migratoria migratorioides* the weight of the vermiform larva is 14 mg. in both sexes. In the first instar, the female becomes heavier than the male, and it continues to be so throughout all subsequent instars. Imago: male 904 mg, female 1251 mg.

The graph of the logarithm of the body mass plotted against instar (including the vermiform larva) is, from the vermiform larva to the first instar, an almost horizontal line, which indicates that growth over this period is almost nil. From the first to the last instar the line is ascending and is almost straight; this indicates that the rate of growth in this period is almost constant. The female graph from the first instar is about the same as the male (fig. 4), but at a higher level.

The specific productivity of growth *(U)* for the whole period of development is, for males 4,168, for females 4,491.

The specific productivity of growth of mass of the body is higher in *Locusta migratoria migratorioides* than in *Schistocerca gregaria,* despite the fact that the average weight in both sexes is greater in the latter. However, the initial weight of the vermiform larva is also greater, which may shift the value of *U*.

In *Schistocerca gregaria gregaria* the weight of the vermiform larva is 20 mg for both sexes. In the first and all subsequent instars the female is heavier than the male. Imago: male 1368 mg, female 1770 mg.

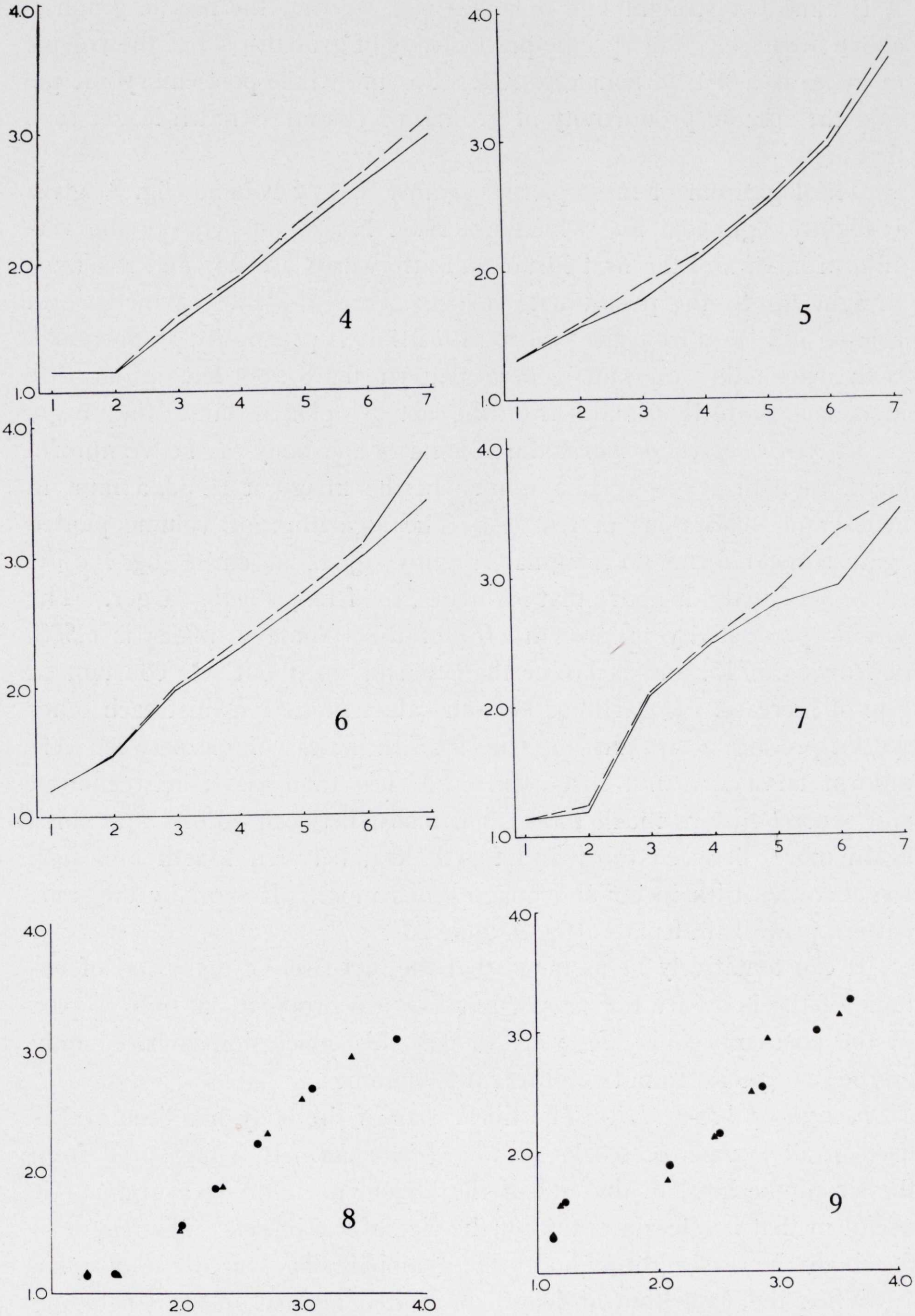
When the logarithm of the mass is plotted against instar the graph rises rather gradually at first, indicating that the mass grows relatively slowly, then rises increasingly steeply to the end (fig. 5). The female graph is above the male.

The specific productivity of growth *(U)* for the whole period is, for males 3,995, for females 4,483.

Generally the larger, heavier species have higher *U* values. In *Melanoplus dawsoni* the average *U* between the first instar and the imago in males is 3,445, in females 3,664; in *Chorthippus parallelus* males it is 2,492, females 2,885; and in *Ch. albomarginatus* males it is 2,167 and females 3,090.

Volume of body (V). The volume is measured by submerging the insect in a liquid and observing the displaced volume. Only for two species are data in this respect available for the whole post-embryonic period.

In *Locusta migratoria migratorioides* the volume of the body of the vermiform instar, in both sexes, is 16,1 mm^3. In the imago, it is 2600 mm^3 in males and 600 mm^3 in females (table 26). When the logarithm of the volume is plotted against instar (including the vermiform larva) the graph is not a straight line; but from the second instar



Figs. 4-9.—4) *Locusta migratoria,* ordinate: logarithm of body mass, abscissa: instar (vermiform larva treated as first instar); male, solid line, female, interrupted line. 5) The same for *Schistocerca gregaria.* 6) *Locusta migratoria,* ordinate: logarithm of body volume, abscissa: instar. 7) The same for *Schistocerca gregaria.* 8) *Locusta migratoria,* ordinate: logarithm of body mass, abscissa: logarithm of body volume. 9) The same for *Schistocerca gregaria* (male: triangles, female: rounds).

it is almost a straight line in males (fig. 6), and the female graph is above the male. The specific productivity of growth *(U)* of the volume in males is 5,084, in females 5,921. For the whole post-embryonic period the specific productivity of growth of volume is much larger than that of mass.

The logarithm of mass plotted against that of volume (fig. 8) gives a slightly sigmoidal line which is almost horizontal between the vermiform larva and the first instar and afterwards ascends and is almost straight up to the penultimate instar. Thus the rate of increase of volume and mass from the first to fifth instar is practically proportional. Both sexes follow the same general pattern (fig. 8), but females increase in volume more than males from the last nymphal instar to the imago.

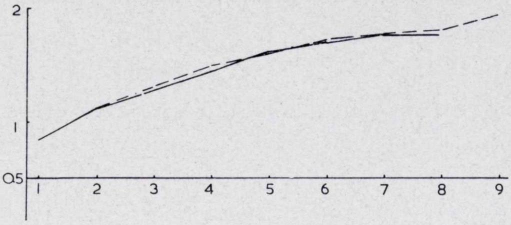
In *Schistocerca gregaria* the volume of the body of the vermiform larva, in both sexes, is 13,5 mm^3. In the imago it is 3325 mm^3 in males and 4098 mm^3 in females. The logarithm of volume plotted against instar forms an irregular, slightly sigmoidal, curve (fig. 7); the curve for females is above that for males, the females being larger. The specific productivity of growth *(U)* of the volume in males is 5,508, in females 5,715, and is larger than that of mass but less constant in rate of increase. Logarithms of both values plotted against each other do not produce a straight line (fig. 9). In males volume between vermiform larva and first instar increases less than mass, between first and second instars much more than mass, between second and third again more, between third and fourth less, between fourth and fifth less, between fifth instar and imago much more. Essentially the same pattern prevails in females (fig. 9, table 23).

It can tentatively be assumed that the increases of mass and of volume of the body are not proportional or are proportional only in part of the post-embryonic life-cycle, though this conclusion is based only on the two species from two different subfamilies.

Length of body (L). The linear size of the body has been and is used in all taxonomic works on *Acridomorpha.* It is measured from the tip of the head to the end of the abdomen. This measurement is useful in that it offers a notion of the size of the insect. The length of the body increases throughout the nymphal stage of *Acridomorpha.*

When the logarithm of length is plotted against instar (including the vermiform larva) an almost straight line results (figs. 10-15) in most of the species with a cylindrical body, which indicates that the linear increase is consistent. In the species with the "straw-like" body the line is less regular (figs. 10-15), deviating at the beginning and the end. The specific productivity of the linear growth is larger in the species with the very elongate body.

Width of body (W). Measurements of the width or height of the body are taken in the widest place. For the majority of species this is the thorax. Separately, this measurement is rarely used, but it is essential for determining the index of the proportion of the body *(Pr)*.



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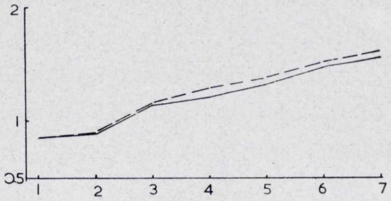

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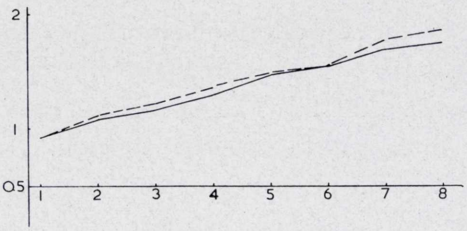

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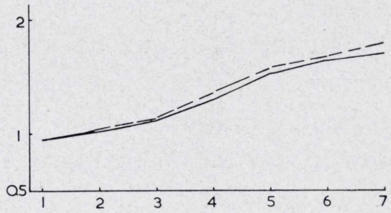

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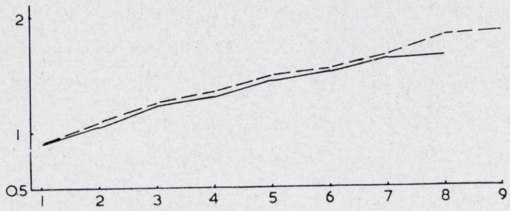

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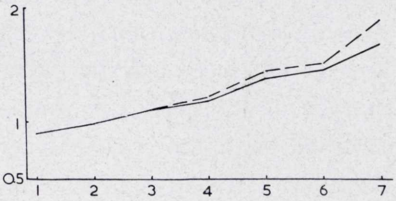

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Figs. 10-15.—Ordinate: logarithm of body length, abscissa: instar (vermiform larva treated as first instar); 10) *Cephalocoema canaliculata;* 11) *Zonocerus variegatus;* 12) *Lobosceliana femoralis;* 13) *Romalea microptera;* 14) *Acrida bicolor;* 15) *Mesopsis gracilicornis.*

When logarithms of width and length of body are plotted against one another they produce an irregular line.

Index of body proportion (Pr). The several principal forms or shape of body can be expressed by an index or proportion, which is useful in that it indicates the general shape of the body more concisely than any other index. It is determined by dividing length *(L)* by width *(W)*. The index of body proportion in species with a "straw-like" body can be as high as 20 (in *Cannula linearis),* while in species with a short, depressed body *(Lathicerus cimex)* it is about 2.

As can be seen from the graphs (figs. 10-15) every species has its own individual pattern of linear growth and it is not possible to establish a general rule for all *Acridomorpha.*

HEAD.

In all cases studied the head of the vermiform larva retains the embryonic position and appearance. Its position corresponds to opistognathous heads in adult *Acridomorpha,* the frons being inclined backwards and the mouth-parts being in a ventro-posterior position. In cases in which the head of the adult insect is opistognathous (e.g. *Keyacris* (fig. 23), *Cephalocoema* (fig. 24), *Acrida* (fig. 46), *Mesopsis* (fig. 50) this position occurs in all instars. For species in which, in the adult stage, the head is hypognathous or prognathous, the embryonic position is equivalent to a bending-down of the whole head so that its longitudinal axis is parallel with that of the body. This position creates a wide gap between the occipital margin of the head and the anterior margin of the head and the anterior margin of the pronotum; this gap is filled with an enlarged cervical membrane which forms a cervical ampulla. The pressure of blood in the ampulla facilitates the rupture of the egg chorion and, in the vermiform larva, the rupture of the cuticle along the existing ecdysial cleavage line; the head then gradually gains its normal position.

The shape of the embryonic head in its apical part is mostly approximately subglobular. In species with hypognathous heads it is more globular (figs. 44, 49), and in those with opistognathous heads it is less so, approximating more to obtusely conical with the apical end rounded (figs. 23, 24).

In the first instar, the head in most cases transforms from the embryonic to more or less the imago shape, as is shown in *Loboscelíana femoralis* (figs. 31, 32), in which the vermiform larva has the widely rounded, subglobular head (fig. 30), whereas the first instar acquires and almost fully adult, short, acutely conical head (figs. 31, 32). When the adult head is subglobular the change of shape is less marked (fig. 49). In cases of elongate, acutely conical, heads in adults, the change of shape takes place in the vermiform larva and during the transformation to the first instar. In *Cephalocoema canaliculata* the head grows in length from its embryonic shape (fig. 24), and thereby changes its proportions, during the first ten minutes after hatching; this growth can be readily observed, like the growing of the wings after the final ecdysis. The same phenomenon occurs in *Mesopsis* (fig. 50).

In *Acrida* (fig. 46) the process of head growth is different. In the vermiform larva the apical part of the head is folded like a concertina (fig. 46) and the growth is a process of unfolding, but we do not know whether this is due to expansion of the cuticle by blood pressure or to stretching of it by growing cells inside the apex of the head. In *Acanthoxia,* the transformation of the head is achieved in a different way; it does not grow rapidly in the vermiform larva, but grows and changes proportions gradually from instar to instar (fig. 42), slowly achieving its grotesque, strongly elongate, adult form (fig. 42).

Jago, 1963, showed that the growth of body mass and that of head width in *Eyprepocnemis plorans meridionalis* are proportional.

FASTIGIAL FURROW.

This character is important in classification in the superfamily *Acridoidea.*

It has been regarded as a primary epicranial suture which has persisted in some families and subfamilies in the imago, but has disappeared in others. However, the latest opinion (Du Porte, 1946; Snodgrass, 1947) is that the so-called epicranial suture is no suture at all. It does not separate the sclerites, and it shows no indication of the place of their fusing. Matsuda, 1965, considered that this "suture" is the ecdysial cleavage line, along which the cuticle is weakened for effecting rupture at ecdysis.

The fastigial furrow is always present in the imago and in all the nymphal instars in the following families and subfamilies: *Pneumoridae, Trigonopterygidae, Xyronotidae, Charilaidae, Pamphagidae, Lathiceridae, Pyrgomorphidae, Ommexechidae.*

In *Eumastacidae* it is present in some genera but absent in others.

In *Acridinae* there is no trace of it in nymphs or adults. A well developed fastigial furrow sometimes occurs in unexpected groups. The genus *Gemeneta* of *Hemiacridinae* possesses such a furrow. In furrowless families and subfamilies, traces of it are noticeable in the early instars.

The present investigation of *Acridomorpha* has led to the conclusion that the fastigial furrow and ecdysial cleavage line are independent formations, the fastigial furrow being a linear invagination of the skeletal structure of the cranial capsule, while the ecdysial cleavage line is a weakened part of the cuticle. In the early instars, however, they are liable to be confused, and in some of the specific descriptions in this work it has been considered appropriate to use the non-committal term "fastigial line".

The meaning of the fastigial furrow from an anatomical point of view is unknown. Possibly it is a skeletal development for strengthening the structure of the cranial capsule. To support this view, it is noteworthy that even in *Pamphagidae* it is more developed in the species with the head conical than in those with the head subglobular.

This character is used for purely phenetic classification, its phylogenetic meaning being unknown. Speculations on its phylogeny cannot be profitable until its development in relation to the internal structure of the cranial capsule has been studied. It should be noted though that the fastigial furrow is present in more primitive and absent in more advanced families and subfamilies.

ANTENNA.

The segmentation of the antenna can be observed in the embryo before hatching, but counting the segments is difficult since, in almost every case, it is difficult to decide whether all the apparent sutures are truly intersegmental. In most cases (table 2) the number of segments increases from instar to instar. There are, however, species in which no changes occur and the imago has the same number of segments as the vermiform larva (e.g. *Keyacris* of *Morabinae)*.

The antenna consists of the scape, pedicel and flagellum. During the nymphal period the scape and pedical change in size but very little in shape or proportion. The major changes occur in the flagellum, whose segments grow in size and also change in proportions and often in shape (fig. 17).

In the vermiform larva in all cases studied the antenna has the same appearance as in the embryo before hatching. It is short and ribbon-like, with indistinct segmentation of the flagellum. The ratio of length to width of the flagellum in the vermiform larva is about 5,5-6,0.

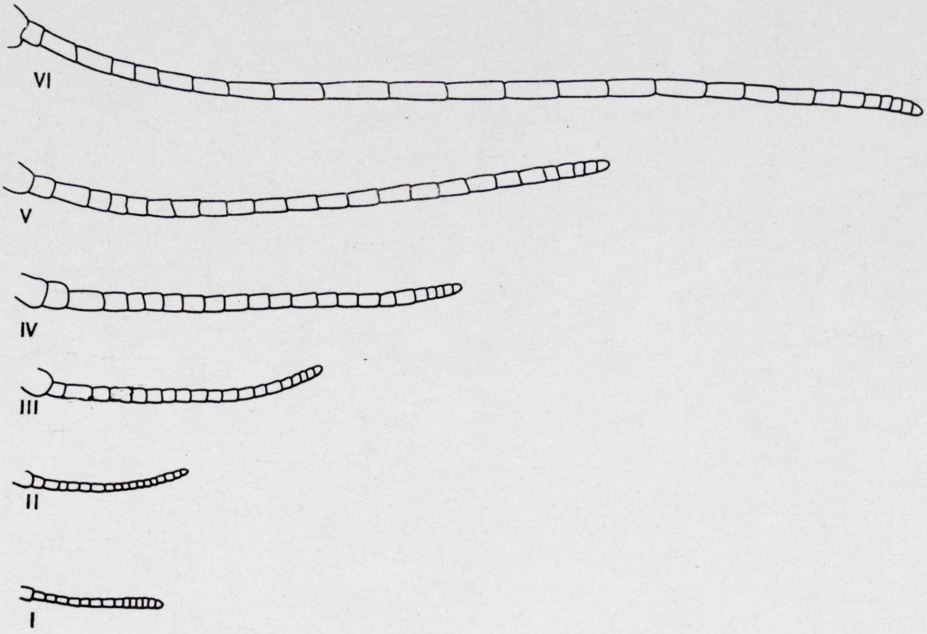

Fig. 16.—Antenna of *Gastrimargus procerus:* I, first instar; II, second instar; III, third instar; IV, fourth instar; V, fifth instar; VI, imago.

At ecdysis between the vermiform larva and the first instar the antenna grows in size, and sometimes in number of segments, and in cases of a flagellum of complicated shape a change in shape occurs also. In *Loboscelíana* (fig. 17) in the first instar the antenna already acquires the complicated shape of that of the imago.

In *Locusta* and *Gastrimargus* (fig. 16) the shape remains almost constant and only the proportions and the number of segments are changed.

The smallest number of antennal segments observed in the first instar is eight, and this number was noted in numerous species, and the largest number is 21, in *Mohavacris* sp. In the imago the smallest observed number of segments is eight and the largest 33 (Mason, 1954).

From Table 2 the conclusion might be drawn that females have more antennal segments than males, but careful studies have shown that the difference, if it exists, is not significant statistically (Mason, 1954).

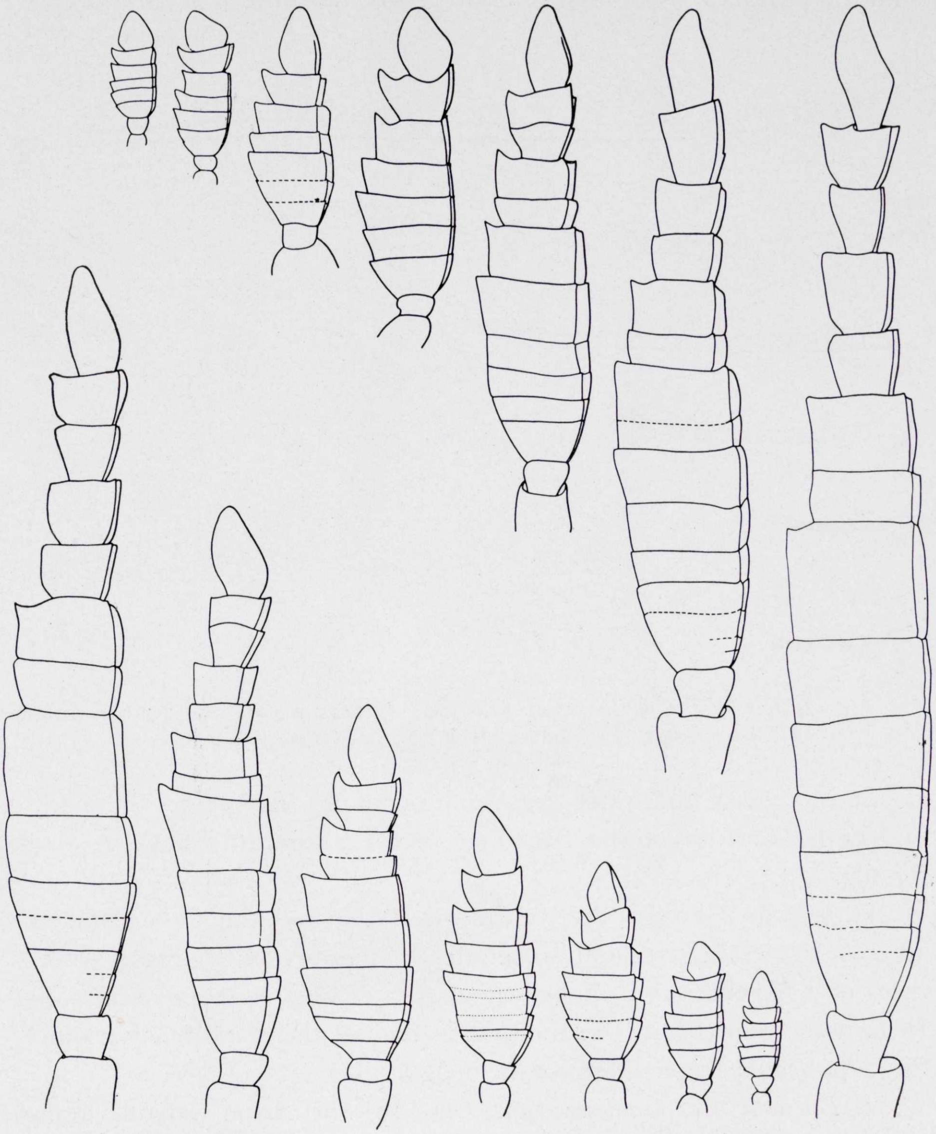

Fig. 17.—Antenna of *Loboscelìana femoralis*. Upper row, female antenna in successive instars, the first instar on the left, the imago on the right; lower row, male antenna in the same sequence but in the reverse direction.

Comparison of the number of antennal segments and body size and length showed that there is no correlation between them. There is

TABLE 2.

Examples of the number of antennal segments in nymphs and adults.

(The segments counted comprise the scape, pedical and flagellum.)

Instars	Vermiform larva		I		II		III		IV		V		VI		VII		imago	
Sexes	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Species																		
Acrida bicolor	10	10	10	10	14	14	14	15	16	16	17	18	18	19	—	19	19	20
Aularches punctatus	—	—	10	10	12	12	14-15	15-16	15-16	15-16	16-17	16-17	16-17	16-17	16-18	16-18	17-18	17-18
Caloptenopsis voltaensis	—	—	13	13	15	15	16	17	22	22	24	25	—	—	—	—	24	25
Cephalocoema canaliculata	8	8	9	9	9	9	9	9	9	9	9	9	9	9	—	10	10	10
Charilaus carinatus	—	—	9	9	10	10	15	15	16	17	17	17	—	—	—	—	17	17
Colemania sphenarioides	—	—	8	8	9-10	9-10	10-12	10-12	13-15	13-15	15-17	15-17	17-18	17-18	—	—	19	20
Eyprepocnemis plorans meridionalis	10	10	10	10	15	15	19	19	19	19	20	21	26	26	—	—	26	27
Eyprepocnemis roseus	—	—	13	13	18-19	18-19	21	21	22-24	22-24	22-26	22-25	—	24-29	—	—	22-25	24-29
Gastrimargus procerus	—	—	13-14	14-15	14-15	16-18	21-22	22-23	23-24	25-26	25-26	27-28	—	—	—	—	26-27	28-30
Keyacris scurra	9	9	9	9	9	9	—	—	—	—	—	—	—	—	—	—	9	9
Lobosceliana femoralis	8	8	8	8	9	9	9	9	9	9	13	13	15	15-16	—	—	14-16	15-17
Locusta m. migratorioides	13	13	19	19	21	21	22-23	22-23	24-25	24-25	24-25	24-25	—	—	—	—	26	27
Mesopsis gracilicornis	12	12	13	13	15	15	17	17	21	21	23	23	—	—	—	—	23	23-24
Parahieroglyphus bilineatus	—	—	13	13	14	14	17-21	17-21	22-24	22-24	23-26	25	24-26	24-27	26-28	26-29	24-28	26-29
Romalea microptera	11	11	12	12	15	15	17	17	18	18	19	19	—	—	—	—	21	21
Schistocerca gregaria	13	13	14	14	19	19	20-21	21	22-23	23	24-25	25	—	—	—	—	26-27	27
Zonocerus variegatus	7	7	8	8	11	11	15	14	18	17	19	19	—	19	—	—	20	20

an indication of some correlation between the degree of wing development and the number of antennal segments. The highest average number was observed in macropterous species and the lowest in the apterous species (Mason, 1954).

The number of segments often differs in the right and left antennae, the difference being of one or two segments (Katiyar, 1953). This asymmetry was observed from the second instar but most frequently occurs in the imago. The superfamily *Eumastacoidea* has the lowest number of antennal segments in both the vermiform larva and the adult. The superfamily *Acridoidea* has the highest on average, in the first instar and the adult, and within this superfamily the families *Pamphagidae* and *Pyrgomorphidae* in the adult stage have, on average, fewer segments than *Acrididae* (Mason, 1954). The other superfamilies are too little studied in this respect. In general, the number of antennal segments varies within a species. The difference may be from one to three segments, as was observed in species of *Acrida* and *Truxalis*. A difference of one or two segments is rather common.

PRONOTUM.

In all the species examined the shape of the pronotum of the vermiform larva is very simple, approximately cylindrical, but more elongate in the species with long narrow bodies. The crest-like shape and other peculiarities, including complicated sculpturing, appear later. A tendency towards the shape which the pronotum will attain in the adult stage begins to appear in the first instar. In cases of a cylindrical or subcylindrical adult pronotum the changes are rather small throughout nymphal development.

In *Lobosceliana* of *Pamphagidae* (fig. 30) the pronotum in the vermiform larva is cylindrical as usual, but in the first instar it acquires an imago shape. In *Gastrimargus,* which in the adult stage possesses a rather high carina, it develops gradually, increasing from instar to instar until it reaches its final shape at the last ecdysis. In *Pneumoridae* the vermiform larva is not known, but in the first instar the pronotum is strongly crested and relatively very large, covering the whole body. It retains this form during the whole nymphal stage, but becomes relatively smaller, acquiring the usual proportion relative to the body as a whole. In *Trigonopterygidae,* only the penultimate instar of *Trigonopteryx* is known; the pronotum in that instar is high-tectiform, almost crested, while in the imago the dorsum of it is flat, with lateral lobes attached at a right angle. In *Charilaidae* the vermiform larva is unknown, but in the first instar the double median carina is clearly apparent and in subsequent instars it merely increases in height. In *Batrachidacris* the pronotum is about the same shape in the first instar as in the imago. In *Chrotogonus* of *Pyrgomorphidae* the sculpture and the widening towards the posterior end of the pronotum develops gradually up to the adult stage. The same gradual process can be observed in *Ommexecha* of *Ommexechidae*.

In *Lentulidae* the vermiform larva pronotum is in most cases remarkably similar to the imago; in cases of the imago being different in this respect the changes are gradual. In *Dericorythinae* the pronotum is subcylindrical in the vermiform larva and the first instar, and not until the second instar does a small tubercle appear in the prozona which in subsequent instars gradually develops into a crest or large tubercle.

It might be concluded that there is no uniform pattern of post-embryonic development of the pronotum in *Acridomorpha*. There are, however, some definite points. In the vermiform larva the pronotum is uniform for all species regardless of the group to which they belong. In the first instar, the majority of species, in many groups, have the pronotum laterally compressed, tectiform, and this shape mostly persists up to the last ecdysis, when it acquires the imago shape. Other patterns of development include acquisition of the adult shape as early as the first instar, gradual change from instar to instar up to the adult stage, and occurrence of a very drastic change at the last ecdysis.

TEGMINA AND WINGS.

The development of tegmina and wings follows the same pattern in all *Acridomorpha*.

In the vermiform larva there are no external indications of the presence of tegmina or wings. In the first instar their rudiments are traceable. In the second instar the lower posterior angles of the mesonotum and metanotum begin to project and to show a streaky pattern, which indicates the future venation. In the next instar the projections are larger, forming definite lobes which are rudiments of the tegmina and wings, the rudimentary veins now becoming more pronounced and more numerous. In the following instar the process continues in the same way (fig. 18).

In the third, fourth or fifth instar, however, there is an occurrence which still lacks a proper explanation. Up to a certain instar the position of the tegmina and wings is such that their future anterior margins are directed downwards. In the next instar they have turned through 180° so that the anterior margins are directed upwards and the former outer surface is towards the body wall. This is allegedly affected by differential growth of the hypodermal cells. The lower part grows faster, making the lobes more wing-like and causing reversal of position (Ivanov, 1947).

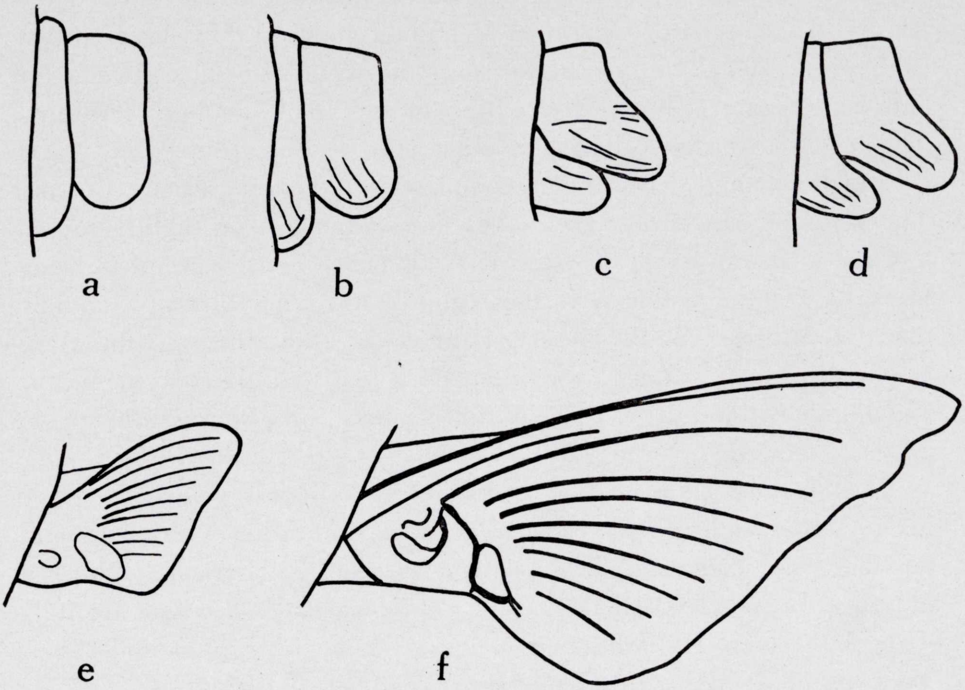

Fig. 18.—Development of wings in *Locustra migratoria*: *a*, vermiform larva; *b*, first instar; *c*, second instar; *d*, third instar; *e*, fourth instar; *f*, fifth instar.

The process may occur in any pre-penultimate instar but has never been observed before the third. Roonwal (1952) considers it as most important in nymphal development and connects it with deep physiological changes. That physiological changes are taking place is indisputable, but the nature of them is far from being known. Webley (1951) has the same opinion, based on counting blood cells in *Locusta migra-*

toria. He observed that in the third instar the number of blood cells increases, and he connected this with an increase of metabolic activity, which is correlated with the turning of the wings. In subsequent instars the number of blood cells drops to the previous level.

That the wing turning always occurs in a particular instar in each species is not proved, since the number of instars is not a rigidly fixed feature of the species. Antoniou & Hunter-Jones (1957) observed that in *Eyprepocnemis plorans meridionalis* the wing reversal occurs at the ante-penultimate ecdysis, irrespective of the total number of instars. This needs to be investigated in other species and groups.

Further wing development comprises gradual increasing in size. The veins become pronounced; they are all straight or slightly curved and are all main veins, no intercalary or cross veins or veinlets being present. At the last ecdysis the tegmina and wings grow so rapidly that the process can be observed directly. Only then do the veins acquire the final pattern; the intercalary veins, if they occur in the species, appear and the cross veins and veinlets of the reticulation appear as well.

It should be noted that in *Xyronotus,* a wingless genus, there are in the ante-penultimate instar some folds indicating the position of possible wing rudiments. These folds, however, disappear at the last ecdysis. In wingless females of *Lobosceliana,* males of which are fully winged, there are also folds suggesting rudiments of tegmina and wings. They disappear in the fifth nymphal instar (Thomas, 1954).

In species which possess some kind of stridulatory mechanism, part of which is located on tegmen or wing, this part appears only during the last ecdysis.

TYMPANAL ORGAN.

Of the fourteen families of *Acridomorpha,* the tympanal organ is normally present in six (table 3). In families in which it is present it is sometimes large and well developed, with a large thin membrane; on the other hand, it may be small, with the membrane rather strongly sclerotised, or even reduced to a hardly detectable rudiment or completely lost. In the families in which it is normally absent in the adults, no traces of it can be found in the nymphs.

The tympanal organ can be detected in the vermiform larva or first instar as a thin area of the integument on each side of the first abdominal tergite. In the second instar the area has a more definite shape, and may be considered as a distinct structure. Its further development takes place progressively, at the ecdyses.

HIND FEMUR.

The shape and structure of the hind femur provide important taxonomic characters, which are mentioned in every description. They are used as diagnostic characters for families, subfamilies, genera and species.

The shape of the hind femur in adults is extremely variable. Some femora are narrow, elongate, straw-like, and almost square in cross-section *(Acrida, Truxalis)*, with a ratio of length to width reaching 21,0. At the other extreme are femora which are flattened laterally and strongly widened, with a ratio of length to width of about 2,0 *(Plagiotriptus)*. The hind femur may be of a peculiar shape, heavily sculptured, and equipped with spines, teeth and expanded edges. In the vermiform larva, however, it is usually a simple, narrow, laterally flattened structure, without armour or sculpture. *Lobosceliana,* which in the imago possesses flattened and expanded hind femora, is exceptional in this respect; even on hatching, the hind femur is flattened, slightly expanded and with detectable serration on the upper carina. Changes towards the adult shape are gradual and take place during ecdysis.

The growth of the femur is sometimes proportional to body growth but in other cases it is irregular.

Basal lobes of hind femur. The lower basal lobe of the hind femur, in adults, may be longer than, shorter than, or equal to the upper basal lobe. This character is used in classification of the higher taxa, both families and subfamilies. Out of 14 families of *Acridomorpha* (table 3) seven have the lower lobe, in the imago, longer than the upper; four have it shorter; and in others it may be shorter or longer than the upper or equal to it (table 3).

In the vermiform larva the base of the femur is seldom divided into lobes. In the first instar the division is apparent, and in all families, except *Pauliniidae,* the lower basal lobe of the hind femur is longer. The change to the adult shape and relative dimensions appears in the second or sometimes in later instars.

The question as to whether a longer lower lobe is a more primitive character than equal lobes, or a longer upper one, or whether these characters are not connected with ancestral history, is a difficult one. There are unfortunately no relevant palaeontological data. In the opinion of the present author, however, the longer lower lobe is more primitive, since it is present in the first instar in almost all families.

Brunner's organ. This organ is a small soft tubercle in the basal half of the lower side of the hind femur, usually nearer to the lower internal carina. In cross-section, the outer wall of the tubercle consists of a thin layer of cuticle, below which there is a layer of hypodermal cells. It bears several spine-like, trichoid sensilla of various lengths and several sunken campaniform sensilla. Since the sensilla are connected by neurons with the femoral nerve, it is presumed that they are sensory structures. It has been suggested that the organ itself is connected with the jumping mechanism of the hind legs, but experimental work has failed to provide proof of this and the function of the organ remains obscure.

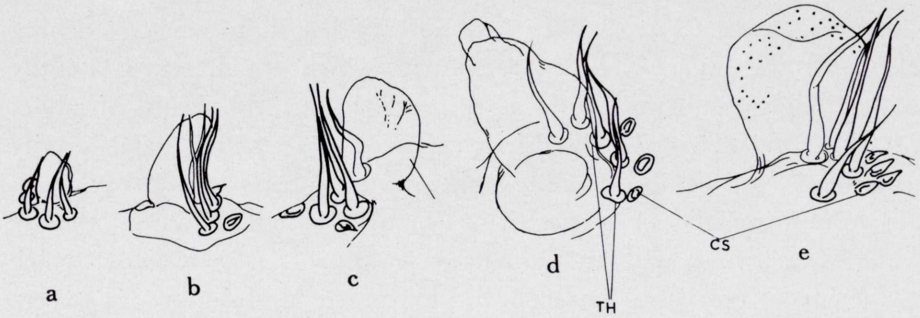

Fig. 19.—Brunner's organ of *Stenobothrus lineatus* (males): *a,* first instar; *b,* second instar; *c,* third instar; *d,* fourth instar; *e,* imago. *TH* — tactile hairs. *CS* — campaniform sensilla (after Roscow, 1963).

In the fourteen families of *Acridomorpha* Brunner's organ is completely absent only in *Proscopiidae,* but it is absent also in some genera of the *Pneumoridae.*

In the families in which it occurs, it can usually be detected in the first instar and with some difficulty in the vermiform larva as well. It has the same trichoid sensilla and rudiments of campaniform sensilla in the nymph as in the adult. From instar to instar it changes very little (fig. 19), only growing in size and proportions. In males, Brunner's organ is relatively smaller and with stouter trichoid sensilla than in females (Roscow, 1963).

Stridulatory serration of hind femur. This part of the stridulatory mechanism is situated on the inner side of the hind femur in various families and groups. It may be a cluster of small tubercles at the base of the inner side of the femur (in *Trachypetrella),* a row of transverse ridges (in *Pneumoridae),* a saw-like row of obtuse teeth, or a row of articulated pegs (in the subfamilies *Truxalinae* and *Eremogryllinae).* Since the stridulation is supposedly connected with sexual activity and attraction, it plays an important part in the survival and life of the

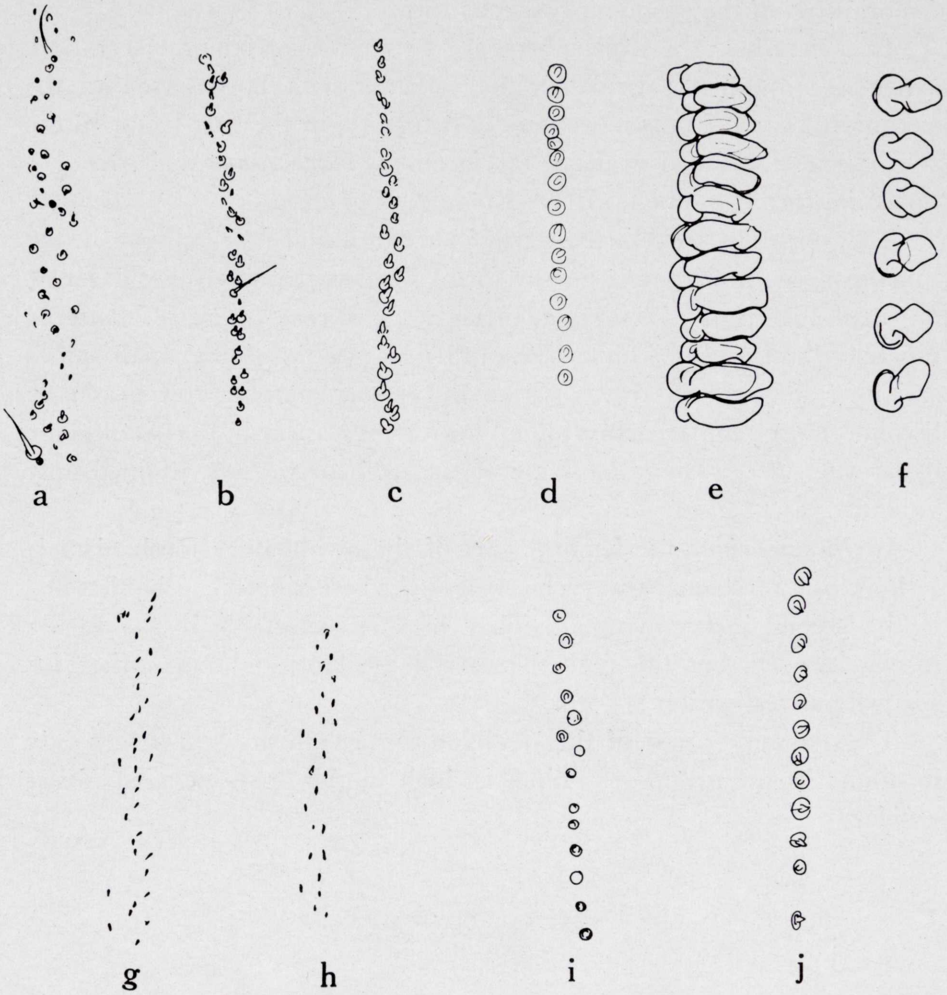

Fig. 20.—Stridulatory serration of *Stenobothrus lineatus. a-f),* male: *a)* first instar; *b)* second instar; *c)* third instar; *d)* fourth instar; *e)* imago, middle of the row of stridulatory serrations; *f)* imago, distal end of the row of stridulatory serrations. *g-j)* female: *g)* first instar; *h)* second instar; *i)* third instar; *j)* fourth instar (After Roscow, 1963, modified).

species. The latest research indicates that there are no families or species which do not produce sounds in one way or another.

In the present work, only the subfamily *Truxalinae* and part of the *Pneumoridae* were investigated in respect of the development of the femoral part of the stridulatory mechanism.

In *Truxalinae,* in which there are two types of femoral serration, articulated and not articulated, the serration can be detected in the vermiform larva. It is more readily detectable in the first instar in the two species examined in detail *Dociostaurus maroccanus* and *Stenobothrus lineatus.* (Jannone, 1939; Roscow, 1963).

The serration seen in the vermiform larva and more clearly in the first instar is, in *Truxalis,* in the form of a comparatively regular row of small tubercles. In *Stenobothrus* it is a row of more scattered tubercles, and in *Dociostaurus* the tubercles are more like small spines and form an irregular row. From instar to instar the row gradually becomes more regular, achieving a linear arrangement in the penultimate instar (fig. 20). The final shape of the teeth or pegs is attained only in adults.

In *Pneumoridae* the femoral part of the stridulatory mechanism is a short row of strong, transverse ridges. These ridges can be detected in the second instar nymph. (They may be detectable in the earlier instars as well, but the limited material available did not suffice for adequate investigation.)

The abdominal part of the stridulatory mechanism is apparent only in adults in the groups examined (which in this case included *Xyronotidae).*

EXTERNAL GENITALIA.

The whole complex of the terminal structures of the abdomen is here referred to as the external genitalia. They include the structures directly connected with copulation and reproduction such as the cerci, subgenital plate and ovipositor, and also parts unconnected with reproduction, such as the supra-anal plate and the paired paraprocts, which cover the anal opening.

In the vermiform larva and sometimes in the first instar, but rarely in the second, the abdominal extremities are directed ventrally (the embryonic position) in such a position as to have occupied as little space

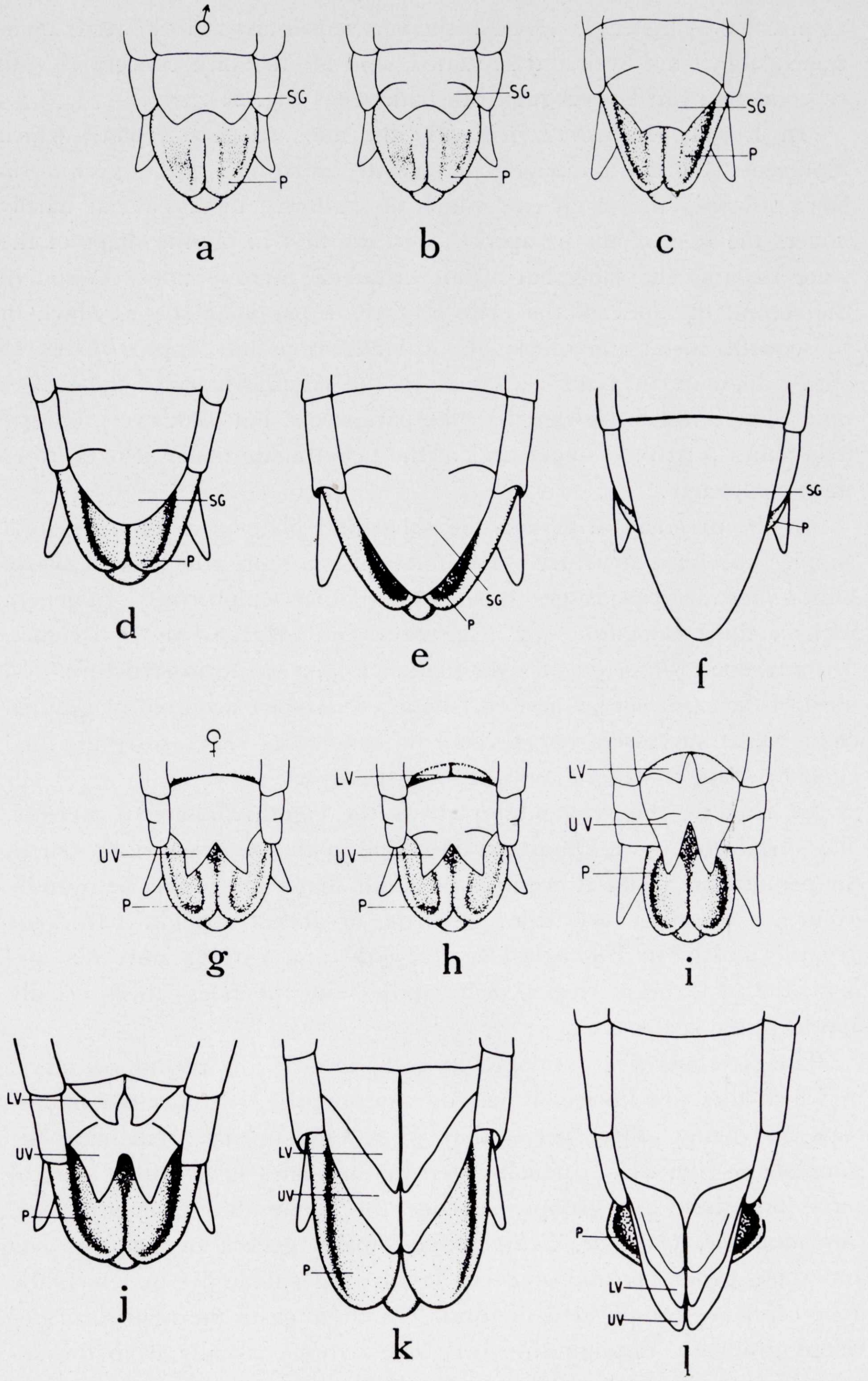

Fig. 21.—Development of external genitalia of *Locusta migratoria migratorioides*. Ventral view. *a-f)* male: vermiform larva to fifth instar, respectively; *g-l)* female: vermiform larva to fifth instar, respectively. (All drawn to different scale).

as possible in the egg. Even in the vermiform larva all the parts mentioned above are well differentiated, and all that are concerned with reproduction can be recognised in both sexes (fig. 21).

In *Locusta migratoria* (fig. 21) the male subgenital plate, which represents the ninth abdominal sternite, narrows in the vermiform larva towards the distal end which is shallowly incurved and hardly covers the base of the paraprocts. In the first instar the shape of the plate remains the same but a pair of lateral furrows appears, and in the second the apex of the plate acquires a parabolic shape, which in subsequent instars becomes elliptical and in adults approximates to obtuse-angular (in ventral view). In the vermiform larva the subgenital plate is much shorter than the paraprocts, but with every ecdysis it becomes relatively longer and in the penultimate instar it overgrows them completely.

In the majority of genera the subgenital plate in adult males is a simple subconical structure. Less often it is a more complicated shape, with a bilobate apex, ridges, tubercles and other sculpturing. In genera with a thin, elongate body (e.g. *Mesopsis, Mesopsera, Betiscoides, Moraba,* some *Proscopiidae)* the plate is a long ensiform structure. In most of the cases studied its final shape and size are acquired by gradual changing at successive ecdyses, but in some cases *(Mesopsis)* the final elongate shape is achieved only at the last ecdysis.

In females, the subgenital plate is the eighth abdominal sternite. The distal end is an almost straight line in the earlier instars, but in the penultimate instar it acquires the adult shape which may be roundly excurved, angular, bilobate or trilobate, or almost straight. In some groups, mostly in *Eumastacidae, Oxyinae* and various unrelated genera, the plate bears ridges, teeth, spines and tubercles; these usually appear at the last ecdysis.

The cerci are well developed in both sexes in the vermiform larva, in which they are invariably narrow and angular. In *Locusta migratoria* and many other species they grow only in size, remaining the same shape (fig. 21). In many genera the males have simple conical cerci, but there are groups, such as the subfamilies *Euryphyminae, Coptacridinae, Oxyinae, Calliptaminae,* many genera of *Catantopinae* and some genera in almost every family and subfamily, in which the male cerci are complicated in form. In these cases the final form develops gradually through the successive ecdyses, usually from the second instar. In *Xyronotus* (fig. 27) the branches of the cercus appear gradually from an undetermined instar, attaining the peculiar final form and length in the imago only.

The dorsal valves of the ovipositor are clearly visible in the vermiform larva as a single undivided metamere, distal to the eighth abdominal sternite. The distal end comprises a pair of angular lobes, which in subsequent instars become the apical ends of the dorsal valves of the ovipositor. The ventral valves of the ovipositor are not visible in the vermiform larva and their position can be determined only by a slight furrow between the distal end of the eighth sternite and the proximal end of the dorsal valves of the ovipositor. In the first instar the ventral valves of the ovipositor appear from the furrow. They are in the form of a pair of transverse lobes. The sclerite of the dorsal valves of the ovipositor grows longer in the first instar, with the apical

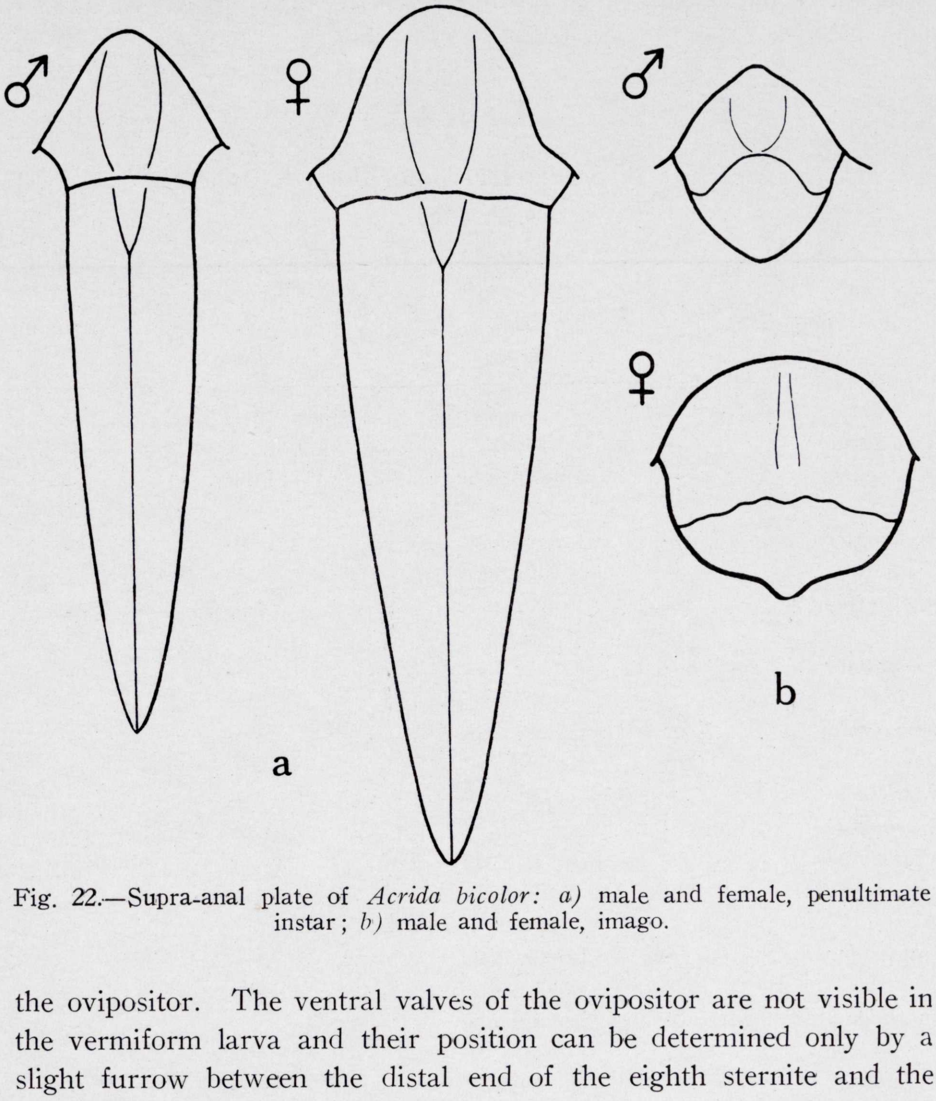

Fig. 22.—Supra-anal plate of *Acrida bicolor: a)* male and female, penultimate instar; *b)* male and female, imago.

lobes more acute-angular and elongate. In subsequent instars both pairs of valves grow considerably, and in the penultimate instar the ventral valves are only slightly shorter than the dorsal ones. In the imago both pairs are about the same length.

The supra-anal plate or epiproct in both sexes represents the eleventh tergite. In adult males, the plate is sometimes peculiarly shaped and sculptured, but usually it is a simple angular structure; in females, it

TABLE 3.

Important characters in adult ***Acridomorpha*** (+ indicates presence, — absence).

Families	Brunner's organ	Lobes of hind femur	Fastigial furrow	Elytra and wings	Tympanum
Eumastacidae	+	Variable	+ or —	+ or —	—
Proscopiidae	—	Lower lobe longer	—	Mainly —	—
Trigonopterygidae	+	Lower lobe shorter	+	+	—
Tanaoceridae	+	Lower lobe longer	—	—	—
Xyronotidae	+	Lower lobe shorter	+	—	—
Pneumoridae	+ or —	Lower lobe longer	+	+	—
Charilaidae	+	Ditto	+	+	+
Pamphagidae	+	"	+	+ or —	Normally +
Pyrgomorphidae	+	"	+	+ or —	Normally +
Ommexechidae	+	Of equal length	+	+ or —	+ or —
Lathiceridae	+	Lower lobe longer	+	—	—
Lentulidae	+	Lower lobe shorter	—	—	—
Pauliniidae	+	Ditto	—	+	+
Acrididae	+	Lower lobe shorter or both of equal length	—	+ or —	+ or —

is almost invariably a simple angular structure. In some genera the supra-anal plate manifests a remarkable regressive development; in the vermiform larva and subsequent nymphal instars, in the genera *Acrida, Truxalis, Truxaloides* and *Mesopsis* and in both sexes (fig. 22), it is a very elongate ensiform structure, whereas at the last ecdysis it is greatly reduced and becomes only a small angularly shaped plate. The most remarkable phenomenon in this respect occurs in *Mesopsis,* in which the subgenital plate of the male is transformed into a very elongate, ensiform structure, at first sight very similar to the lost supra-anal plate; in the female, however, there is no such transformation (fig. 50).

In all the species examined the supra-anal plate gradually increases at every ecdysis, including the last except in the cases mentioned above.

The paraprocts are a pair of ventro-lateral lobes of the epiproct, covering the anal opening from the sides, *i.e.* they are parts of the eleventh tergite as is the epiproct itself. In the adult they are mostly simple lobiform structures, but sometimes they form peculiar projections and even bear some sculpturing.

In the vermiform larva in *Locusta migratoria* (fig. 21), as in all the species examined, the paraprocts are relatively very large and in a horizontal position. In every subsequent instar they become relatively smaller, growing much less than the other structures of the end of the abdomen.

SEXUAL DIMORPHISM.

The occurrence of sexual dimorphism in the imago stage of *Acridomorpha* is well known. The females are nearly always larger than the males and the difference in some cases is extraordinarily great. In *Purpuraria erna* the female is two-and-a-half to three times as long as the male, and in *Truxalis grandis* twice as long. In most species, the difference in body size is not so great, but there are very few instances of the female being on average smaller than the male.

In the vermiform larva, no sexual dimorphism in linear dimensions has yet been recorded and none was discovered in the present work, but a difference in weight has been detected in newly hatched *Locusta* and *Schistocerca,* the females being heavier (Blackith, 1961). In the first instar, and still more in the second, a difference in size has been detected, females usually being larger, though in one instance males were found to be longer than females in the first instar (table 5).

Sexual dimorphism is conspicuous in nymphs of those species in which the adult males are fully winged and the females are completely apterous. Good examples of this can be found in the subfamily *Porthetinae* of *Pamphagidae*. There are also many species in which the males are macropterous and the females brachypterous or micropterous as in *Pneumoridae,* some genera of *Echinotropinae, Akicerinae* of *Pamphagidae* and *Charilaidae,* and in these cases also the dimorphism is very evident in the later nymphal instars.

The antennae sometimes display great sexual dimorphism in adults. In *Taramassus,* the segments of the apical third of the male antenna have strong leaflike expansions, whereas in females they are almost filiform. A similar phenomenon occurs (but in different shape) in *Cyathosternum.* Both these genera belong to the subfamily *Eyprepocnemidinae.* In the subfamily *Porthetinae* sexual dimorphism is evident in the number and to some extent the shape of the antennal segments. In some genera of the group *Gomphocerini* of *Truxalinae* the male antennae are widened club-wise at the apex, while in females the antennae are only slightly widened. This kind of sexual dimorphism, however, is not noticeable in nymphs and becomes evident only after the last ecdysis.

The anterior tibiae in the males of the genus *Gomphocerus* are inflated, almost pear-shaped; in females they are of normal shape.

The elytro-femoral stridulatory mechanism, which is present in all *Truxalinae,* is much more developed in males than in females (fig. 20) even in the early instars (Roscow, 1963). Sometimes the males and females differ in type of sound-producing mechanism, as in *Pneumoridae* (Dirsh, 1965). In the genus *Hoplolopha* (subf. *Porthetinae* of *Pamphagidae)* males possess the elytro-femoral sound-producing mechanism, but the apterous females rub their femora against the rugose sides of the abdomen, producing an entirely different kind of noise.

Superfamily **EUMASTACOIDEA.**

Family **EUMASTACIDAE.**

Subfamily ***Morabinae.***

Keyacris scurra (Rehn, 1952) (fig. 23, table 4) was studied as the only representative of the family available in the early instars.

Vermiform larva. Body elongate, cylindrical, of the same size in both sexes. Head obtusely conical with short fastigium of vertex; fastigial furrow absent. Ocelli hardly detectable. Antenna nine-segmented. Pronotum subcylindrical. Lower lobe of hind femur slightly longer than upper. Brunner's organ detectable. External apical spine of hind tibia present. Dorsal serration on basal tarsal segment not detected. Cerci folded (embryonic position). Subgenital plate short in both sexes.

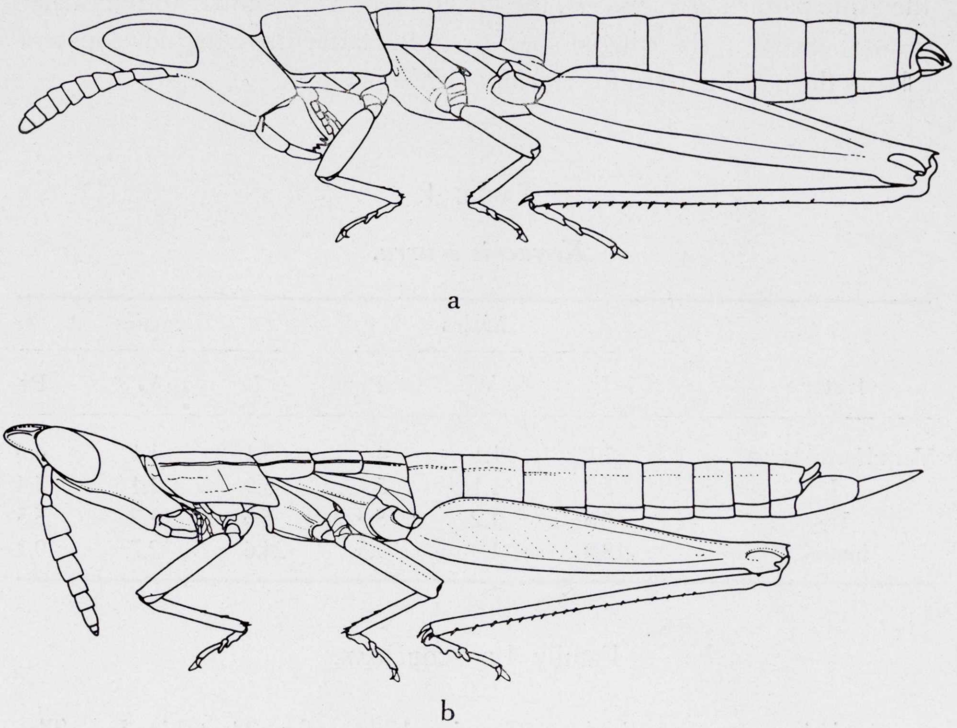

Fig. 23.—*Keyacris scurra*, male: *a)* first instar; *b)* imago.

First instar. Differs from vermiform larva in longer and relatively narrower body, slightly more elongate head and more acute and more elongate fastigium.

Second instar. Differs from the first only in increase of body length and increasing index of body proportion *(Pr), i.e.* body becomes more slender. Cerci straightened to their imago shape.

Lack of material for the remaining instars prevents analysis of the body growth. The index of body proportion continues to increase, being largest in the imago.

The general external morphological characters remain unchanged from the vermiform larva to the imago, except for the secondary sexual characters which develop in the usual way for *Acridomorpha*. The imago retains the nymphal appearance to such an extent that even the number of antennal segments remains unchanged.

The specific productivity of linear growth from vermiform larva to imago is in males 1,809, in females 2,473.

The fragmentary data available for the genera *Thericles* (subf. *Thericleinae)* and *Euschmidtia* (subf. *Euschmidtiinae)* show essentially the same pattern as *Keyacris*, the imago being very similar to the earlier instars, except in the winged species; in the latter the wing development follows the usual pattern for *Acridomorpha*.

TABLE 4.

Keyacris scurra.

	Males			Females		
Instar	L	W	Pr	L	W	Pr
Vermiform larva	5,1	1,1	4,6	5,1	1,1	4,6
I	5,9	1,1	5,4	5,9	1,1	5,4
II	6,6	1,2	5,5	6,6	1,2	5,5
imago	18,0	1,9	9,5	24,6	2,7	9,1

Family PROSCOPIIDAE.

Cephalocoema canaliculata (Guerin, 1844) (fig. 24, table 5). The only available representative of this family was studied.

Males usually have six nymphal instars, females six or seven (after the vermiform larva).

Vermiform larva. Body narrow, elongate, of the same size in both sexes. Head short, conical; fastigium of vertex short, obtuse, length about one-fifth of that of compound eye; fastigial furrow absent. Antenna eight-segmented. Ocelli relatively large. Cervical ampulla very large. Pronotum subcylindrical. Lower basal lobe of hind femur protruding more than upper. Brunner's organ absent. Supra-anal plate and cerci in embryonic position. Sexes distinguishable only by the secondary sexual characters, which in the first instar are not very clear but can be determined on microscopical preparation.

The duration of the vermiform larva is on average about ten minutes.

In the course of it and during the following ecdysis, the growth of the head and particularly of the fastigium is so rapid that it can be observed with the naked eye.

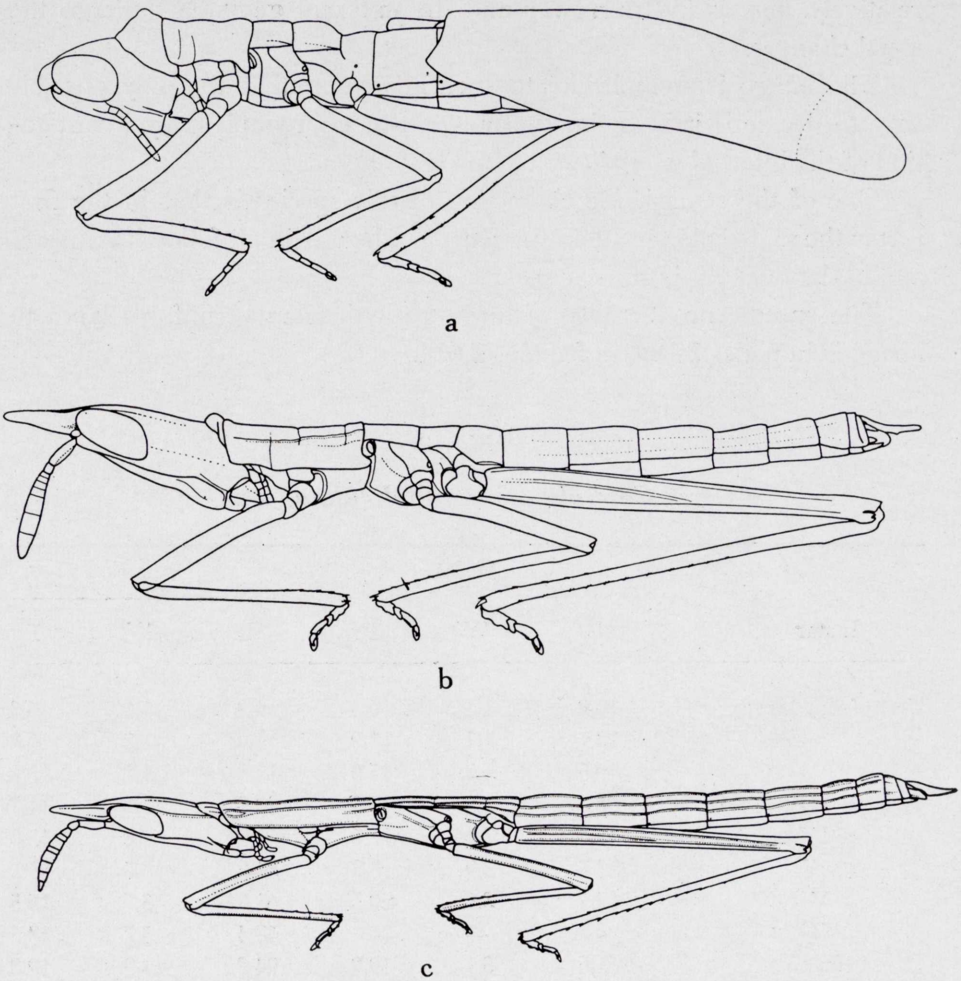

Fig. 24.—*Cephalocoema canaliculata: a)* vermiform larva emerging from egg; *b)* first instar, ten minutes after hatching; *c)* imago, male.

First instar. Body narrow, elongate, relatively narrower than in first instar, slightly longer in male than in female. Head elongate, acutely conical. Fastigium of vertex long, narrow-acute, as long as length of compound eye. Fastigial furrow absent. Antenna nine-segmented. Ocelli as large as in vermiform larva. Cervical ampulla greatly reduced. Pronotum cylindrical, relatively longer than in vermiform larva. Supra-anal plate and cerci in imago position. Secondary sexual characters clearly distinguishable.

All subsequent instars are basically the same shape as the first instar, but the body becomes relatively thinner (table 5), the head and pronotum relatively longer and narrower and the external genitalia undergo the usual changes.

The imago is nymph-like to such an extent that the only possible way to decide if it is an imago or a last-instar nymph is by investigation of the internal genitalia.

One of the remarkable characters of this species is that in the first instar the male is longer than the female, whereas in all following instars and in the imago it is shorter.

The specific productivity of linear growth from vermiform larva to imago is in males 2,189, in females 2,614.

TABLE 5.

Cephalocoema canaliculata.

Instar	Males			Females		
	L	W	Pr	L	W	Pr
Vermiform larva	6,9	1,1	6,3	6,9	1,1	6,3
I	13,1	1,1	11,9	12,9	1,2	10,8
II	19,5	1,3	15,0	19,8	1,5	13,2
III	28,6	1,8	15,9	30,8	2,1	14,7
IV	42,3	2,4	17,6	41,9	2,8	15,0
V	52,7	2,9	18,2	54,6	3,6	15,2
VI	62,1	3,0	20,7	61,0	3,7	16,5
VII	—	—	—	68,4	3,7	18,5
imago	61,6	3,1	19,9	94,2	4,9	19,2

Superfamily TRIGONOPTERYGOIDEA.

Family TRIGONOPTERYGIDAE.

Only very scanty material of this family was available: one female nymphal specimen of a pre-penultimate instar of *Trigonopteryx* sp. and a few nymphs of the last nymphal instar, probably of the genus *Systella* (fig. 25).

All the nymphs studied resemble the adult stage in all respects, except the shape of the pronotum. In the last nymphal instar the pronotum is strongly compressed, the dorsum being narrow tectiform. In the imago of both *Trigonopteryx* and *Systella* the dorsum of the pronotum is flat, with the lateral lobes attached at right angles.

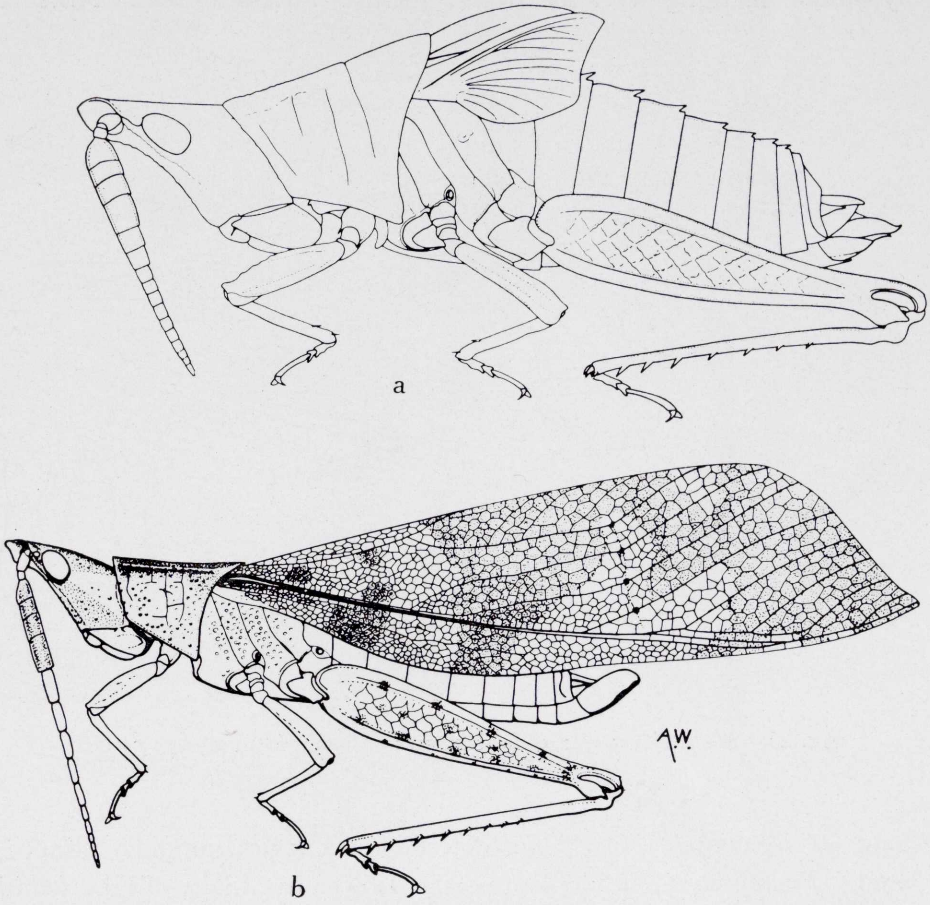

Fig. 25.—*Trigonopteryx* sp.: *a)* nymph in penultimate instar, female. *Trigonopteryx hopei; b)* imago, male.

Superfamily PNEUMOROIDEA.

Family TANAOCERIDAE.

Only scanty material for this family was available. The supposedly first-instar nymph and the imago of *Mohavacris timberlakei* Rehn, 1948, were studied (fig. 26, table 6).

The number of nymphal instars remains unknown.

First instar. Body subcylindrical, slightly compressed. Head subconical, hypognathous; fastigium of vertex strongly shortened, practically absent, merging with the frons; fastigial furrow absent. Antenna long, 21-segmented. Ocelli not detectable. Cervical ampulla disappeared. Pronotum slightly compressed. Lower basal lobe of hind femur longer than upper. Brunner's organ present. Supra-anal plate and cerci in imago position, external sexual characters distinguishable.

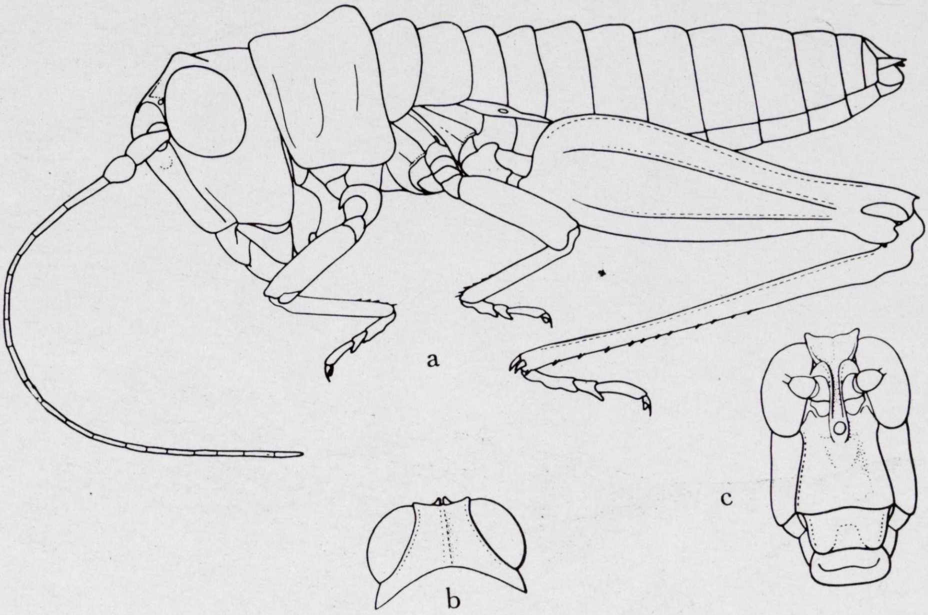

Fig. 26.—*Mohavacris* sp.: *a)* first instar; *b)* head, from above; *c)* face.

The imago is very similar to the first instar. It differs in the 27-segmented antenna of the male, in a relatively less elongate body, in a smaller index of proportion, and in a relatively longer and narrower hind femur. Abdomino-femoral stridulatory mechanism present in male imago, absent in first instar. The imago has a nymphal appearance.

The specific productivity of linear growth, from first instar to imago, is in males 0,470, in females 1,345.

TABLE 6.

Mohavacris timberlakei.

	Males			Females		
Instar	L	W	Pr	L	W	Pr
I	6,3	1,5	4,1	—	—	—
imago	10,0	2,8	3,6	23,0	4,7	4,9

Family XYRONOTIDAE.

This family is one of the least studied. It contains one genus and two species (the second of which was discovered by Prof. J. Cantrall, but has not yet been described).

The species studied here is *Xyronotus aztecus* (I. Bolívar, 1884) (fig. 27, table 7). The material is extremely scanty.

Except adults, only the last nymphal instar and the preceding instar are known. The total number of instars in not known.

Penultimate nymphal instar. Body strongly compressed laterally. Antenna in male ten-segmented. Head short, acutely conical, almost the same shape as in imago; fastigium of vertex same shape as in imago, with similar fastigial furrow. Ocelli poorly developed. Pronotum strongly compressed laterally, lateral carinae noticeable in prozona. Folds indicating place of wings present. Lower basal lobe of hind femur longer than upper. Stridulatory serration on inner side of hind femur present. Brunner's organ well developed. Abdominal stridulatory ridges absent. Male cercus bifurcate.

Last nymphal instar. Differs from penultimate nymphal instar in that the body is even more compressed, the male antenna is 12-segmented, and the male cercus trifurcate. All other characters as in previous instar.

The imago differs from the two previous instars in the still more compressed body; in the greater number of antennal segments which is in males 15-16, in females 17-18; in the more developed lateral carinae in the prozona of the pronotum; in the development of the stridulatory

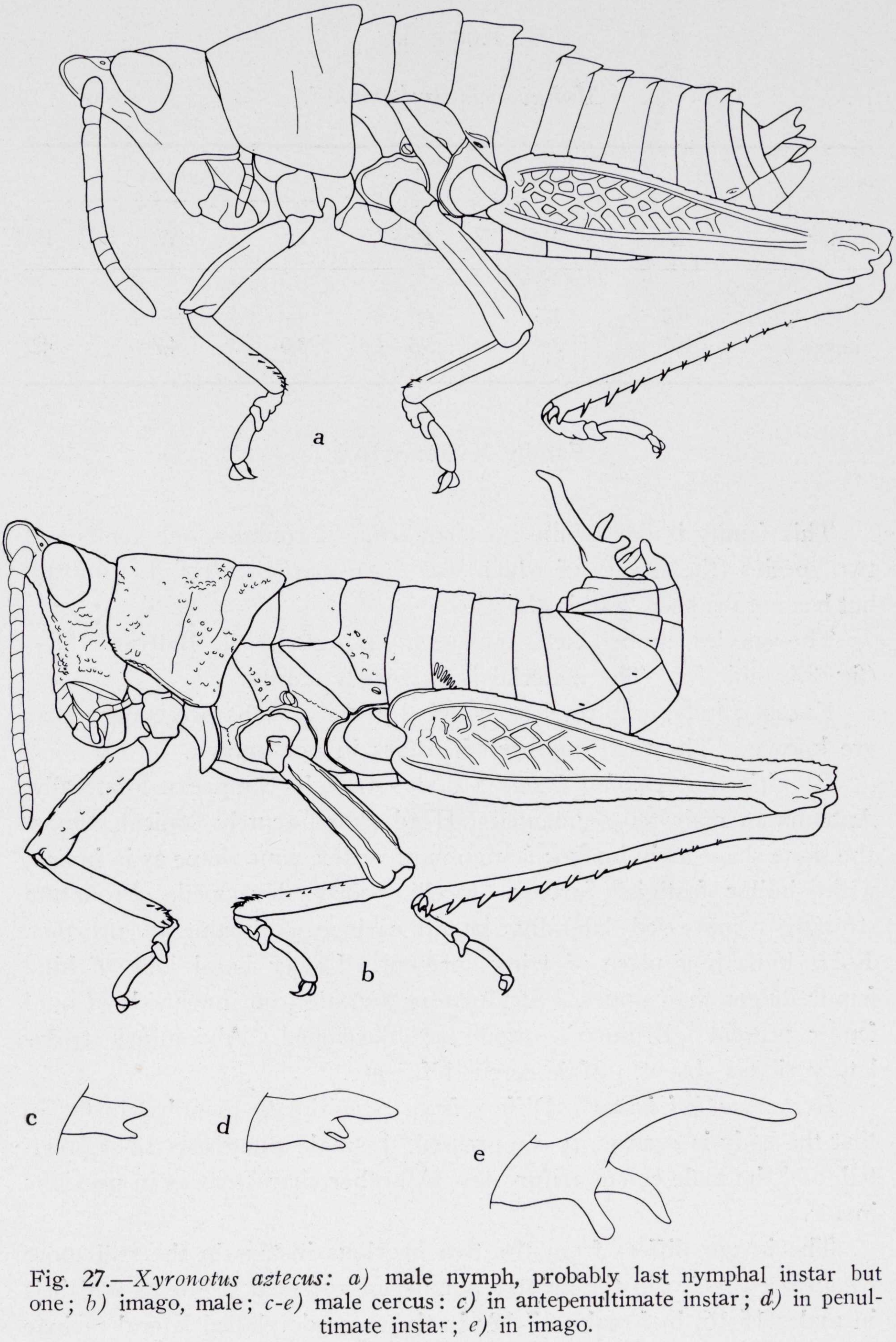

Fig. 27.—*Xyronotus aztecus: a)* male nymph, probably last nymphal instar but one; *b)* imago, male; *c-e)* male cercus: *c)* in antepenultimate instar; *d)* in penultimate instar; *e)* in imago.

ridges on the third abdominal tergite; and in the basal lobes of the hind femur, the lower being slightly shorter than the upper. The male cercus is trifurcate, but with grossly enlarged branches (fig. 27).

TABLE 7.

Xyronotus aztecus.

	Males			Females		
Instar	L	W	Pr	L	W	Pr
Penultimate nymphal	13,0	3,9	3,3	—	—	—
Last nymphal	16,4	4,4	3,7	—	—	—
Imago	17,7	5,1	3,5	27,0	7,7	3,5

Family PNEUMORIDAE.

Only for *Physophorina livingstoni* (Westwood, 1874) and only for the first, second and third instars, were nymphs available (fig. 28, table 8). (Some nymphs of later instars of some unidentified species were also examined and were found not to differ in essential features from *Physophorina)*. The exact number of instars is not known.

First instar. Body compressed. Head, including face, fastigium of vertex and fastigial furrow, as in adult. Antenna 14-segmented. Ocelli hardly detectable. Pronotum relatively very high, crest-like, arcuate, strongly laterally compressed, covering whole body from above; lateral carinae absent, four transverse sulci detectable. Lower basal lobe of hind femur longer than upper, as in adult. Brunner's organ hardly detectable. The abdomino-femoral stridulatory mechanism not detectable.

Second instar. Essentially as first, except in size and in that stridulatory serration on inner side of hind femur (but not on abdomen) now present.

Third instar. Approximately the same as second except in size. Pronotum still covering whole body above.

The main changes which take place in the nymphal development are: — growth of the whole body, with the pronotum growing relatively

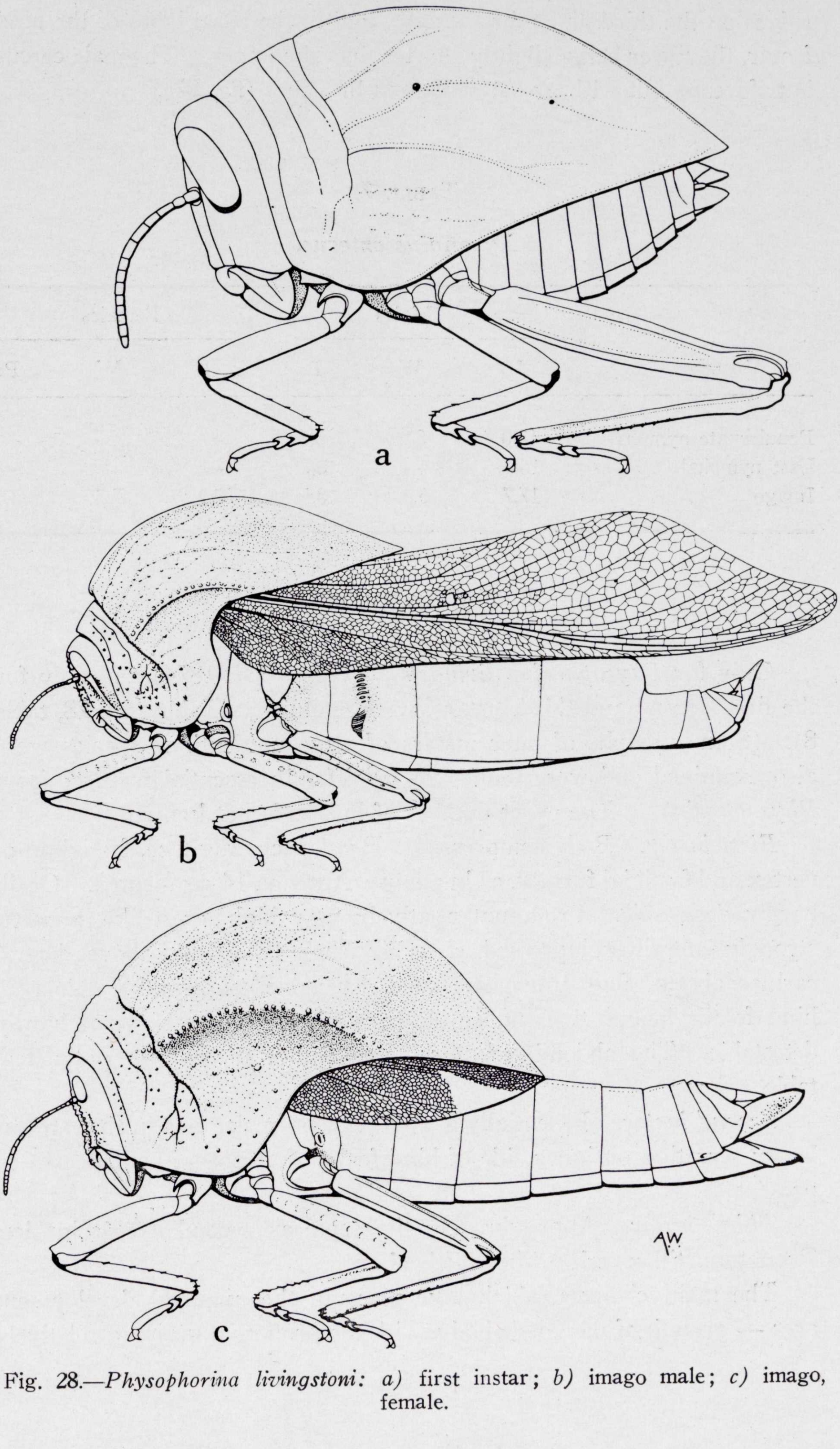

Fig. 28.—*Physophorina livingstoni: a)* first instar; *b)* imago male; *c)* imago, female.

less; increase in the number of antennal segments which in adults of both sexes reaches 24; development of the ocelli, which are hardly detectable in the first instar, but are relatively very large in the male adult, though vestigial in the female; development of wings, and of external parts of the genitalia; development of the abdomino-femoral stridulatory mechanism, the abdominal part of which, consisting of ridges on either side of the third abdominal tergite of the male, appears only in the imago, whereas the femoral part appears in the second instar.

The specific productivity of length of body from first instar to imago is in males 2,217, in females 2,388. The corresponding index for the length of the pronotum is 1,597 and 2,063.

It can be concluded that, at least in the species studied, the post-embryonic ontogeny is more complicated and the nymphs differ more from the imago in *Pneumoridae* than in the other families so far considered.

TABLE 8.

Physophorina livingstoni.

Instar	Males			Females		
	L	W	Pr	L	W	Pr
I	9,0	5,0	1,8	—	—	—
II	14,2	7,2	2,0	—	—	—
III	20,6	13,5	1,5	—	—	—
imago	75,5	28,3	2,7	98,0	39,5	2,5

Superfamily ACRIDOIDEA.

Family CHARILAIDAE.

The species studied was *Charilaus carinatus* (Stål, 1875) (fig. 29, table 9).

Five nymphal instars and the imago were examined.

First instar. Body approximately cylindrical. Head acutely conical, more acute than in imago. Antenna nine-segmented. Fastigium of vertex considerably protruding, parabolic; fastigial furrow as long as fastigium, deep, narrow. Ocelli detectable. Pronotum subcylindrical;

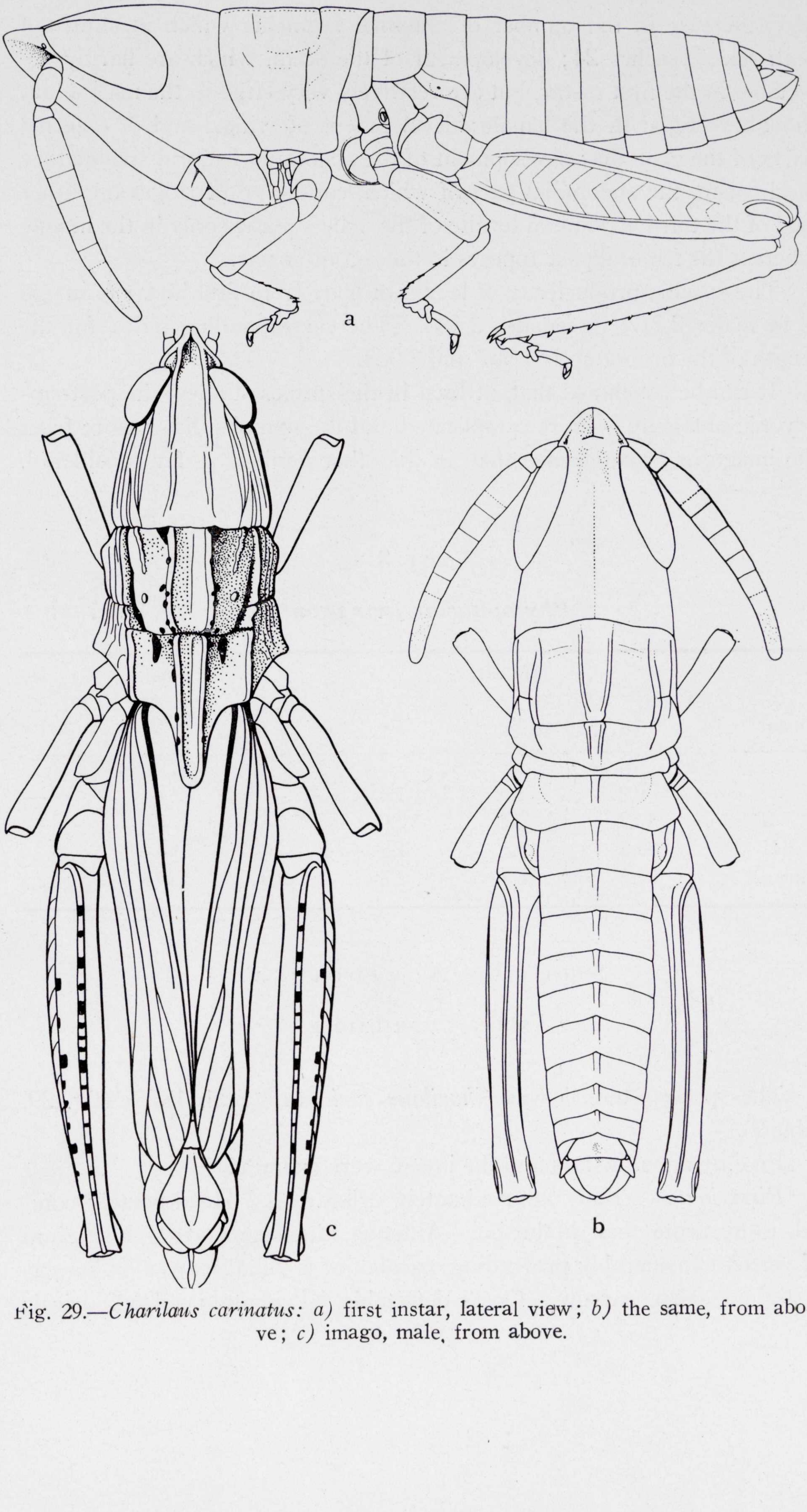

Fig. 29.—*Charilaus carinatus: a)* first instar, lateral view; *b)* the same, from above; *c)* imago, male, from above.

double median carina pronounced; metazona about one-third of length of prozona, its posterior margin slightly protruding in the middle. Prosternal process well developed, of the same shape as in imago. Tympanum detectable. Lower lobe of hind femur longer than upper. Brunner's organ detectable. External apical spine of hind tibia present.

There are no striking changes during the nymphal development from the first instar to the imago, only gradual ones. It should be noted that the number of antennal segments (table 2) increases very little from instar to instar generally very little from the first instar to the imago. Most of the features characteristic of the family are present in the first instar.

The specific productivity of linear growth from the first instar to the imago is in males 1,163, in females 1,326.

TABLE 9.

Charilaus carinatus.

	Males			Females		
Instar	L	W	Pr	L	W	Pr
I	7,5	2,0	3,8	7,7	2,0	3,8
II	11,0	3,0	3,7	11,0	3,0	3,7
III	14,8	4,0	3,7	17,7	4,8	3,7
IV	18,5	4,5	4,1	21,8	5,1	4,3
V	21,2	5,1	4,2	24,2	7,1	3,4
imago	24,0	6,0	4,0	29,0	9,6	3,0

Family PAMPHAGIDAE.

Subfamily *Porthetinae*.

Only one species of this family, *Loboceliana femoralis* (Walker, 1870), of the subfamily *Porthetinae*, was studied (figs. 30-32, table 10).

The species has six nymphal instars (after the vermiform larva).

Vermiform larva. Body cylindrical. Head, in profile and from above, parabolic, apex broadly rounded; above cylindrically rounded; fastigium of vertex roundly merging with frons; fastigial furrow traceable; ocelli hardly traceable. Antenna ribbon-like; shape of the segments uniform; number of segments not distinguishable. Pronotum cylindrical; no traces of crest; posterior margin straight. Prosternal

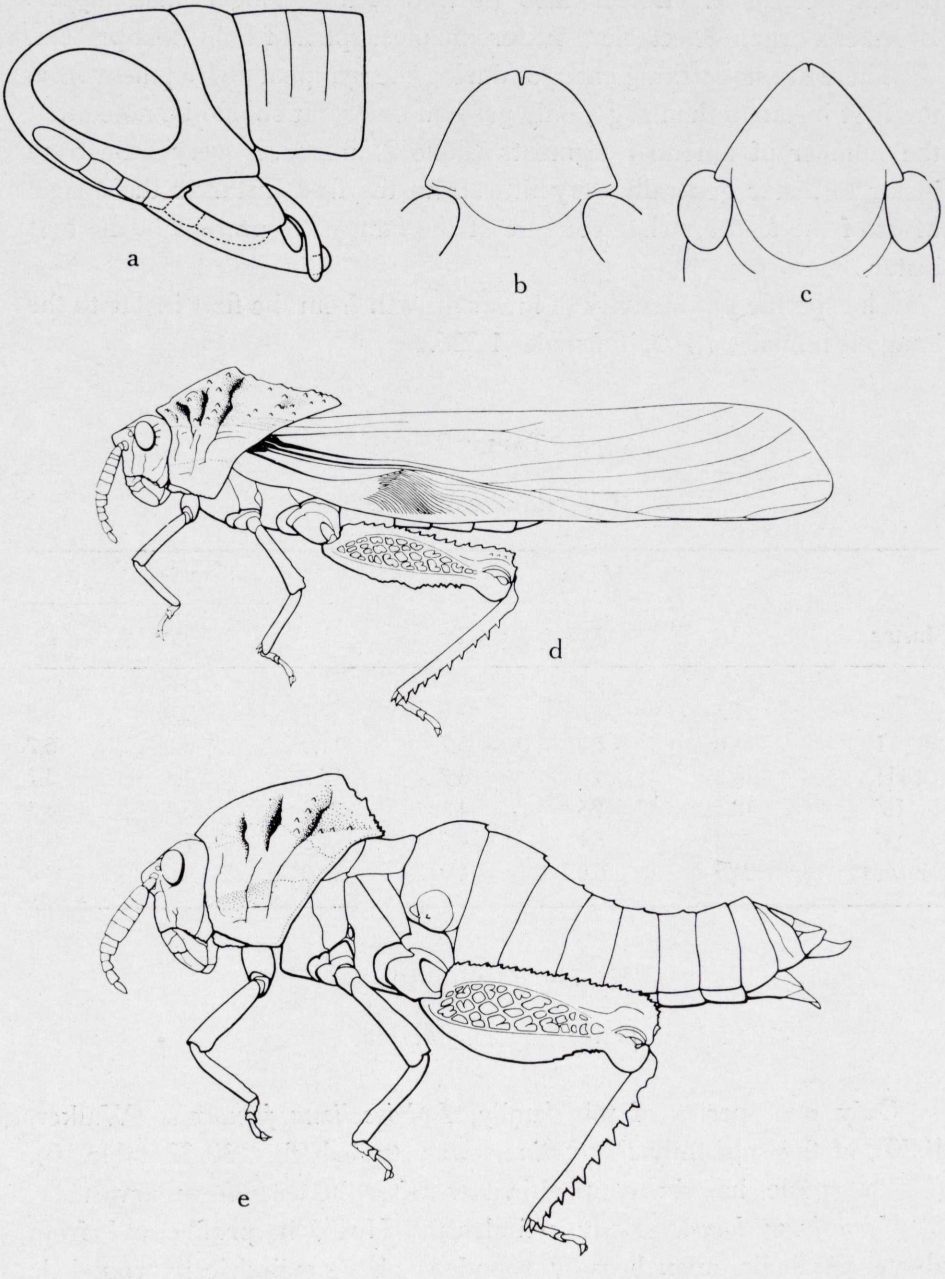

Fig. 30.—*Lobosceliana femoralis:* *a)* head and pronotum of vermiform larva, newly hatched (note shape of head, antenna and pronotum); *b)* fastigium of vertex of first instar; *c)* the same of male imago; *d)* imago, male; *e)* imago, female.

process and tympanum hardly detectable. Hind femur flattened and slightly widened, lower basal lobe longer than upper, upper margin of femur faintly serrated; Brunner's organ traceable. External apical spine of hind tibia present.

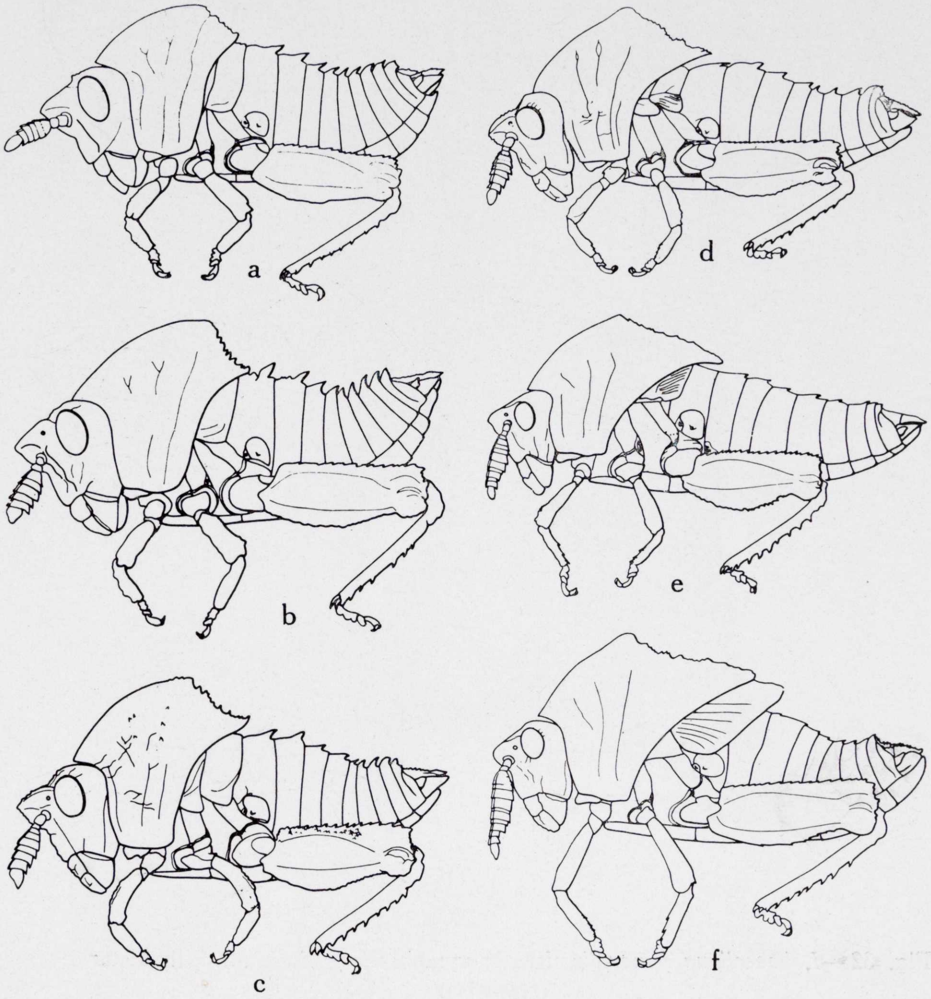

Fig. 31.—*Lobosceliana femoralis,* male nymphs: *a-f)* first to sixth instars, respectively.

First instar. Body compressed. Head conical; apex in profile acute, angular; fastigium of vertex at apex rounded; fastigial furrow short, deep and comparatively wide; frons much less inclined backwards than in vermiform larva. Ocelli present. Antenna (fig. 17) eight-segmented in both sexes, differentiated; flagellum widened, narrow-trian-

*

gular in cross section; apical segment well separated from rest of flagellum; scape and pedicel well separated. Pronotum crested, with crest high and strongly compressed; posterior margin angular. Prosternal process well developed, bilobate. Tympanum clearly visible. Hind femur strongly flattened and widened; lower basal lobe longer than upper; upper margin roughly serrated. Brunner's organ well developed. External apical spine of hind tibia present.

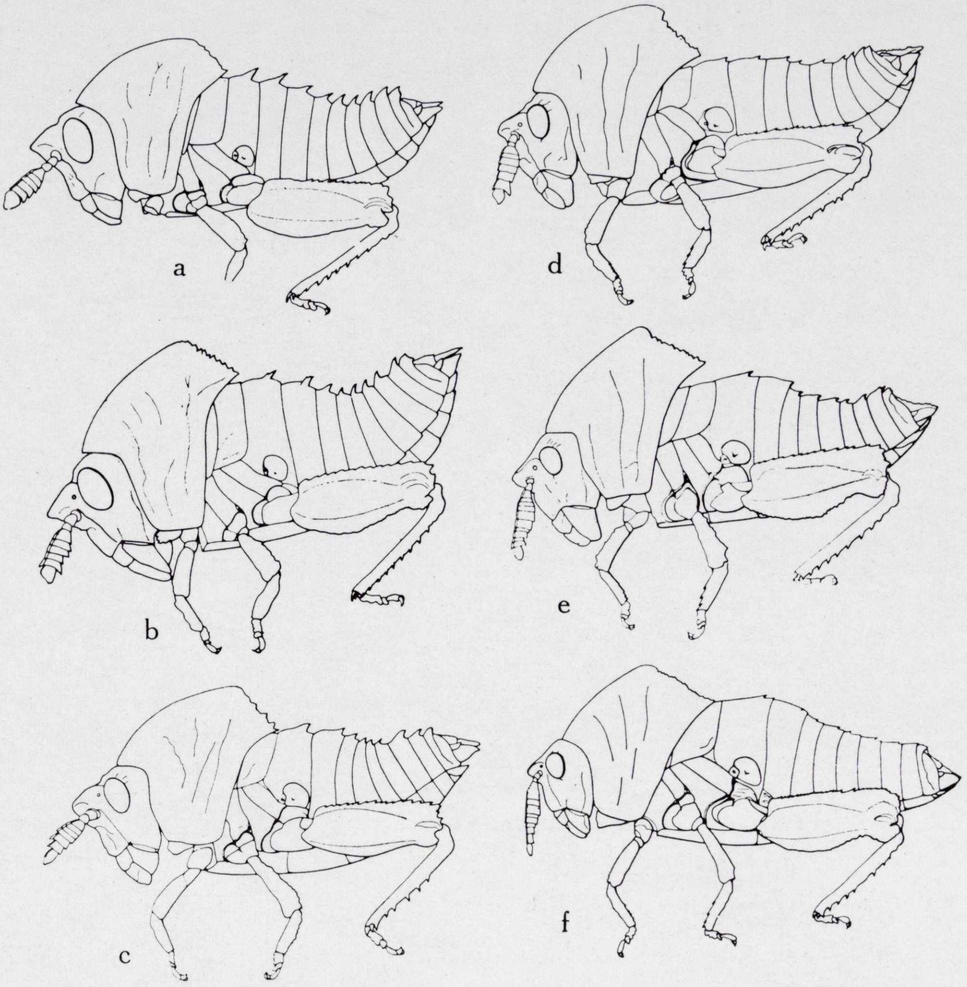

Fig. 32.—*Lobosceliana femoralis,* female nymphs: *a-f)* first to sixth instars, respectively.

The first instar has, almost completely, the appearance of the imago, except for the absence of wings in the male, the undeveloped external genitalia and the number of antennal segments.

All subsequent instars are essentially the same shape as the first and the index of body proportion *(Pr)* remains nearly constant in all instars after the vermiform larva. There is a gradual development of characters, but with the abdomen growing faster than the pronotum. The wings in the male, and the external genitalia and ovipositor, follow the usual pattern of development. The number of antennal segments increases, the flagellum being divided into basal, middle and apical parts. All these changes are gradual, except for the rapid growth of the wing in the male in the last ecdysis. All the essential characters of the family are very well expressed from the first instar.

The specific productivity of linear growth from the vermiform larva to the imago is in males 1,894, in females 2,123.

TABLE 10.

Lobosceliana femoralis.

	Males			Females		
Instar	L	W	Pr	L	W	Pr
Vermiform larva	8,2	2,0	4,1	8,2	2,0	4,1
I	11,9	5,2	2,3	12,6	5,5	2,3
II	14,0	6,4	2,2	16,3	7,5	2,2
III	19,0	8,8	2,2	22,6	10,4	2,2
IV	28,4	11,4	2,5	29,7	13,5	2,2
V	33,7	13,1	2,6	33,7	15,7	2,1
VI	47,8	21,8	2,2	56,6	22,0	2,6
imago	54,5	19,5	2,8	68,5	18,9	3,6

Family PYRGOMORPHIDAE.

Chrotogonus homalodemus (Blanchard, 1836) was studied (fig. 33, table 11).

The number of nymphal instars varies from five to six in males and from five to seven in females (after the vermiform larva).

Vermiform larva. Body cylindrical. Head obtusely conical; fastigium of vertex parabolic; fastigial furrow short and wide; fastigial areolae detectable; ocelli detectable. Antenna eight-segmented. Pronotum subcylindrical, its posterior margin slightly incurved, almost straight. Tympanum hardly detectable. Lower basal lobe of hind femur longer than upper. Brunner's organ detectable. External apical spine of hind tibia absent.

First instar. Body subcylindrical, slightly depressed. Head acute-conical; fastigium of vertex obtuse-angular; fastigial furrow short and deep; fastigial areolae well developed. Ocelli readily detectable. Antenna eight-segmented. Pronotum subcylindrical, its posterior margin slightly incurved, almost straight. Tympanum detectable. Lower basal lobe of hind femur longer than upper. Brunner's organ detectable. External apical spine of hind tibia absent.

All subsequent nymphal instars show gradual development of all characters and are essentially very similar to the adult insect.

The index of body proportion *(Pr)* increases from instar to instar, which indicates that the body becomes more elongate.

Specific productivity of linear growth from vermiform larva to imago is in males 1,337, in females 1,656.

All the features characteristic of the family are present in the vermiform larva.

TABLE 11.

Chrotogonus homalodemus.

	Males			Females		
Instar	L	W	Pr	L	W	Pr
Vermiform larva	4,2	1,3	3,2	4,2	1,3	3,2
I	5,4	1,6	3,4	5,4	1,6	3,4
imago	16,0	3,8	4,2	22,0	5,5	4,0

Zonocerus variegatus (Linnaeus, 1758) (fig. 34, table 12) was studied as a second representative of the family *Pyrgomorphidae.*

Five nymphal instars in males and six in females were observed in this species (after the vermiform larva).

Vermiform larva. Body almost cylindrical. Head obtusely conical with apex rounded; fastigium of vertex short, parabolic; fastigial furrow short and wide. Traces of ocelli present. Antenna seven-segmented. Pronotum subcylindrical. Prosternal process absent. Tympanum de-

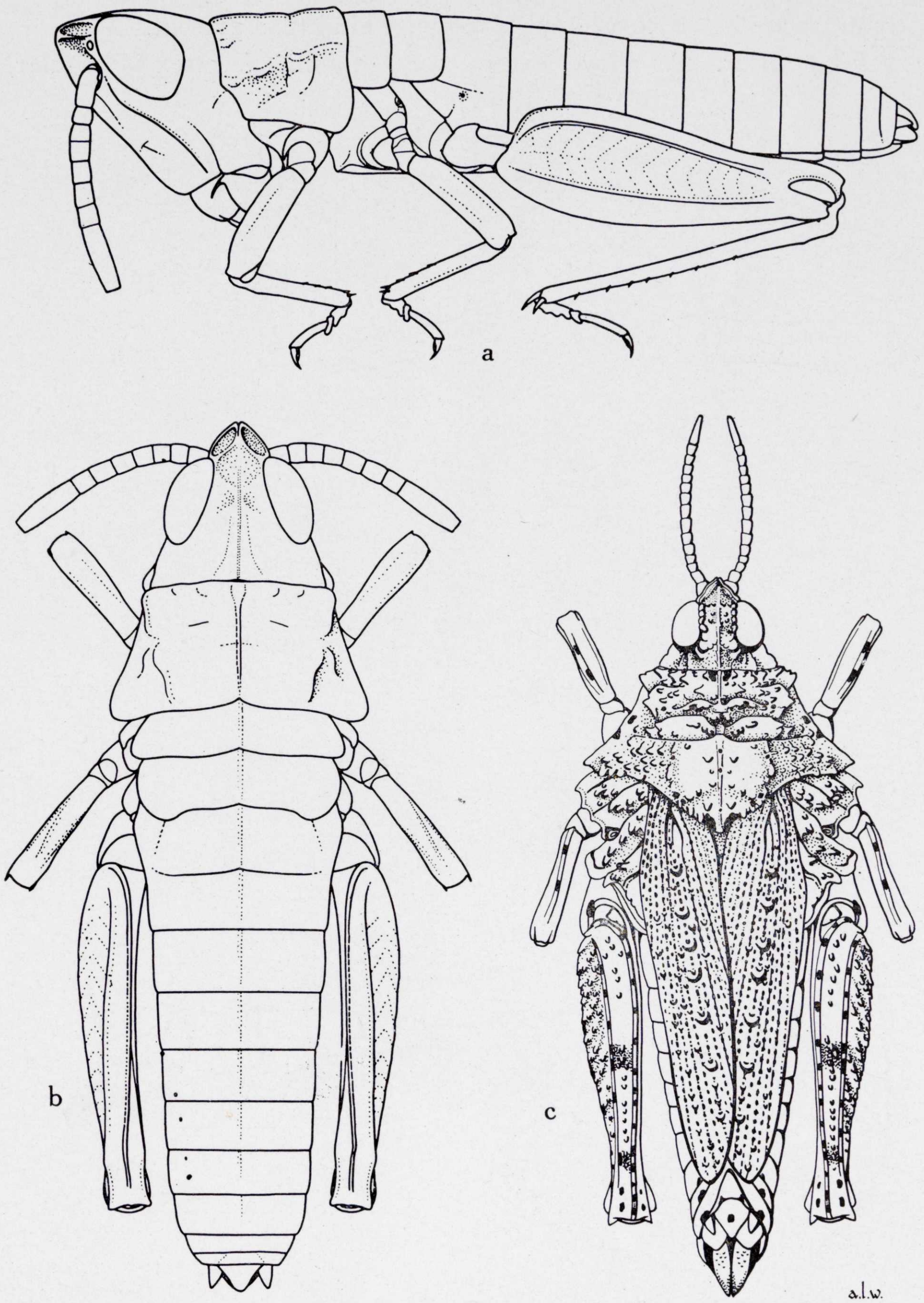

Fig. 33.—*Chrotogonus homalodemus: a)* first instar, lateral view; *b)* the same, from above; *c)* imago, female.

tectable. Lower lobe of hind femur longer than upper. Brunner's organ traceable. External apical spine of hind tibia present.

First instar. As above, except that fastigium of vertex is angular,

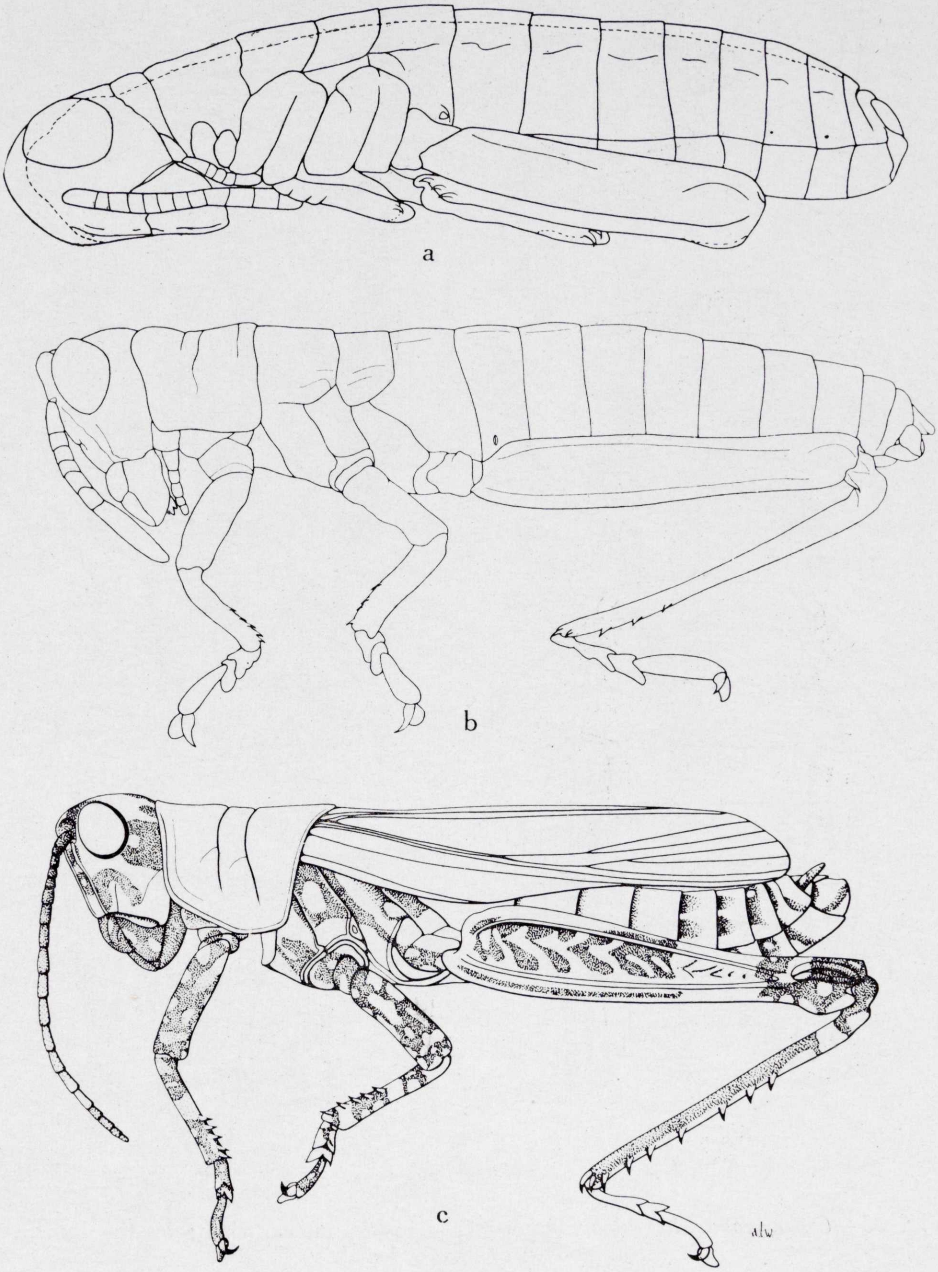

Fig. 34.—*Zonocerus variegatus: a)* vermiform larva (note that apolysis is in progress); *b)* first instar; *c)* imago, male.

whole head more conical and antenna eight-segmented. There is no difference between the sexes except in the external genitalia.

The subsequent instars display only increase in size and gradual development of the first instar characters. The number of antennal segments increases in every instar. The pronotum becomes more tectiform at each ecdysis except the last, when it becomes rather flattened dorsally in the adult.

The index of body proportion increases from the vermiform larva to the imago, but irregularly.

The specific productivity of linear growth from vermiform larva to imago is in males 1,624, in females 1,743.

TABLE 12.

Zonocerus variegatus.

	Males			Females		
Instar	L	W	Pr	L	W	Pr
Vermiform larva	7,0	2,1	3,3	7,0	2,1	3,3
I	7,8	2,6	3,0	8,0	2,6	3,1
II	13,7	2,8	4,9	14,2	3,0	4,7
III	16,4	3,6	4,6	19,0	4,3	4,4
IV	21,0	7,0	3,0	23,2	7,0	3,3
V	29,6	7,3	4,1	32,1	7,6	4,2
imago	35,5	7,3	4,9	40,0	8,8	4,5

Family OMMEXECHIDAE.

Ommexecha servillei (Blanchard, 1836) (fig. 35, table 13) was studied.

The number of nymphal instars is unknown.

First instar. Body subcylindrical. Head irregularly subglobular; fastigium of vertex very short, wide, sloping forwards and roundly merging with frons; fastigial furrow hardly apparent. Ocelli well developed. Antenna ten-segmented. Pronotum irregularly subcylindrical, its posterior margin incurved. Prosternal process absent. Tympanum detectable. Lower basal lobe of hind femur longer than upper.

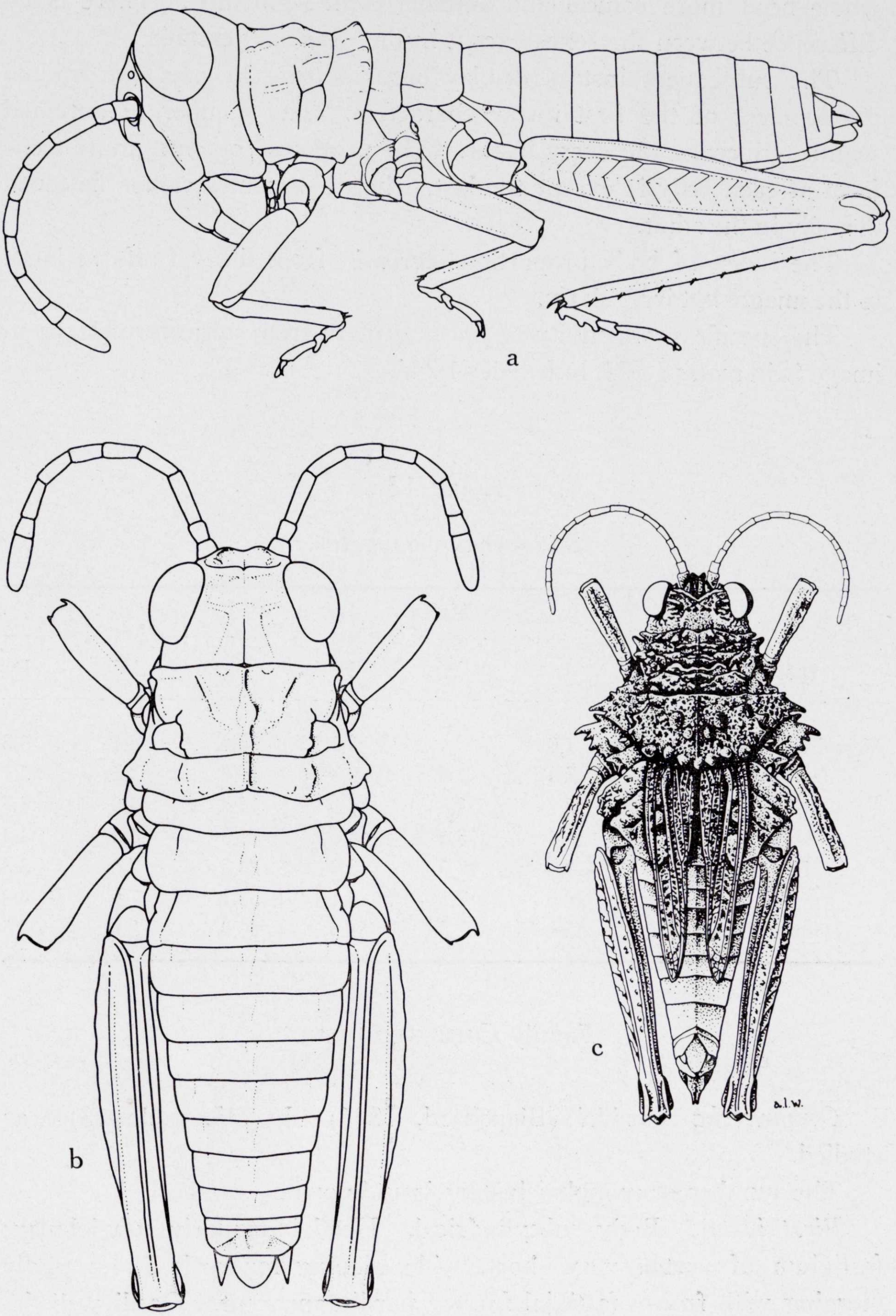

Fig. 35.—*Ommexecha servillei: a)* first instar, lateral view; *b)* the same, from above; *c)* female, imago.

Brunner's organ clearly visible. External apical spine of hind tibia absent.

The first instar differs from the imago in that the integument is not sculptured; in the shape of the head, which in the imago is conical; in the shape of the fastigium which is angular in the imago; and in the virtual absence of the fastigial furrow which is present in the imago.

The specific productivity of linear growth, from the first instar to the imago is in males 1,259; in females 1,460.

TABLE 13.

Ommexecha servillei.

	Males			Females		
Instar	L	W	Pr	L	W	Pr
I	4,6	1,6	2,9	4,6	1,6	2,9
imago	16,2	7,6	2,1	19,8	9,3	2,1

Family LATHICERIDAE.

Batrachidacris rubridens (Uvarov, 1929) (fig. 36, table 14) was studied.

First instar. Body depressed, short and stout. Head subglobular; fastigium of vertex very short, hardly projecting in front of eyes; fastigial furrow short, but well developed; antennal grooves present, but rather shallow. Antenna eight-segmented. Ocelli not detectable. Pronotum wide, subcylindrical, its posterior margin slightly excurved, almost straight. Prosternal process not detectable. Hind femur widened; its lower basal lobe longer than upper. Brunner's organ detectable. External apical spine of hind tibia absent.

The index of body proportion *(Pr)* decreases from the first instar to the imago.

The first-instar nymph in its essential features is similar to the imago.

The specific productivity of linear growth from first instar to imago is, in males, 1,455.

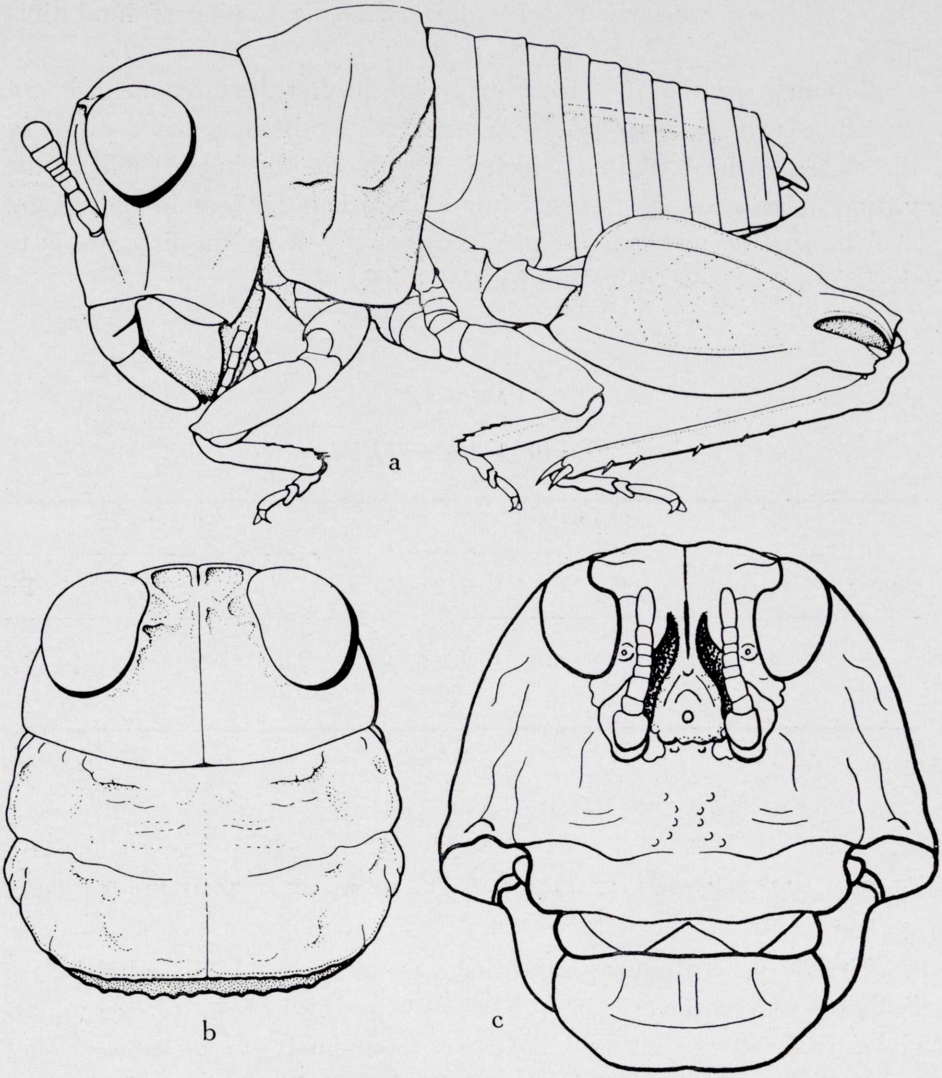

Fig. 36.—*Batrachidacris rubridens: a)* first instar; *b)* head and pronotum from above of first instar; *c)* face of male imago (note the antennal grooves).

Table 14.

Batrachidacris rubridens.

Instar	Males L	Males W	Males Pr	Females L	Females W	Females Pr
I	7,0	2,5	2,4	—	—	—
imago	30,0	14,2	2,1	36,0	19,7	1,8

Family LENTULIDAE.

Mecostibus sp. (fig. 37, table 15) was studied.

The number of instars is unknown.

First instar. Body subcylindrical. Head subglobular; fastigium of vertex short and wide, slightly protruding in front of eyes, at apex slightly incurved, roundly merging with frons; fastigial line present but weak. Ocelli well developed. Antenna 13-segmented. Pronotum cylindrical with straight posterior margin. Tympanum completely absent. Lower basal lobe of hind femur about same length as upper. Brunner's organ detectable. External apical spine of hind tibia absent. Coxal process of middle leg present.

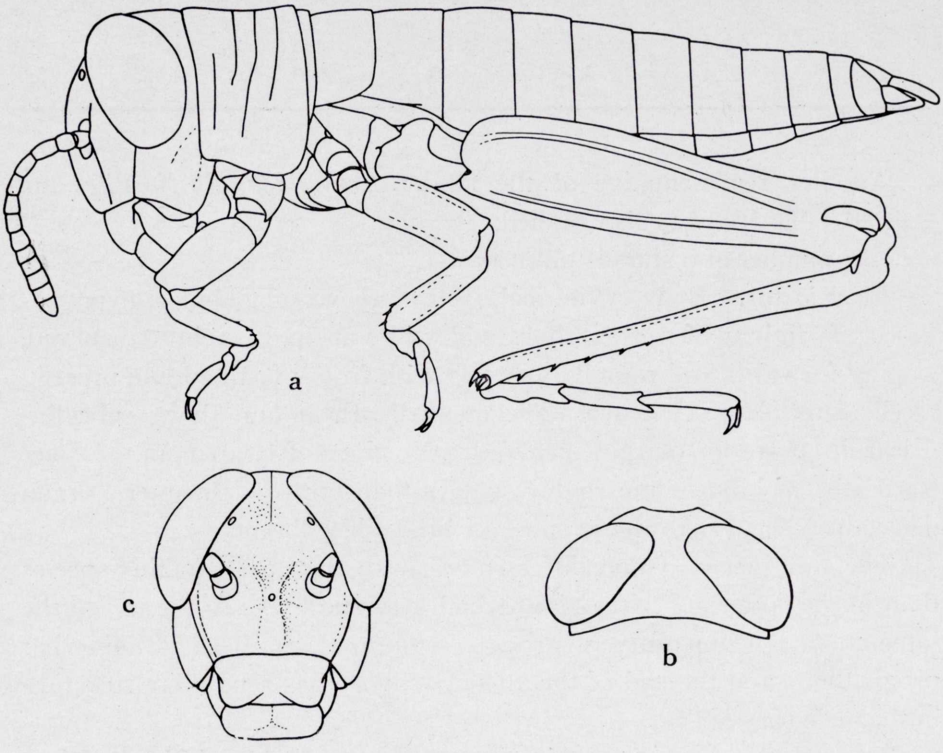

Fig. 37.—*Mecostibus* sp., first instar: *a)* lateral view; *b)* head from above; *c)* face.

It is remarkable how little the first-instar nymph differs from the imago.

The specific productivity of linear growth from the first instar to the imago is in males 1,016, in females 1,378.

TABLE 15.

***Mecostibus* sp.**

Instar	Males L	Males W	Males Pr	Females L	Females W	Females Pr
I	6,3	1,5	4,2	6,3	1,5	4,2
imago	17,4	3,5	5,0	25,0	4,5	5,0

Another representative of the family *Lentulidae, Shelfordites* sp. (fig. 38, table 16), was also studied.

The number of instars is unknown.

First instar. Body cylindrical. Head above subglobular, hypognathous; fastigium of vertex short and wide, at apex slightly incurved, sloping forwards and roundly merging with frons; fastigial line present. Ocelli detectable. Antenna 12-segmented. Pronotum short, subcylindrical, its posterior margin incurved. No trace of tympanum. Lower basal lobe of hind femur slightly longer than upper. Brunner's organ detectable. External apical spine of hind tibia absent.

The first-instar nymph differs more from the imago in this species than in the species of *Mecostibus* which was studied. In the imago the integument is comparatively strongly sculptured, the head is somewhat prognathous and the end of the abdomen above has a peculiar structure in the male (fig. 38).

The specific productivity of linear growth is in males 0,916, in females 1,358.

TABLE 16.

***Shelfordites* sp.**

Instar	Males L	Males W	Males Pr	Females L	Females W	Females Pr
I	3,6	1,1	3,3	3,6	1,1	3,3
imago	9,0	2,1	4,3	14,0	3,1	4,5

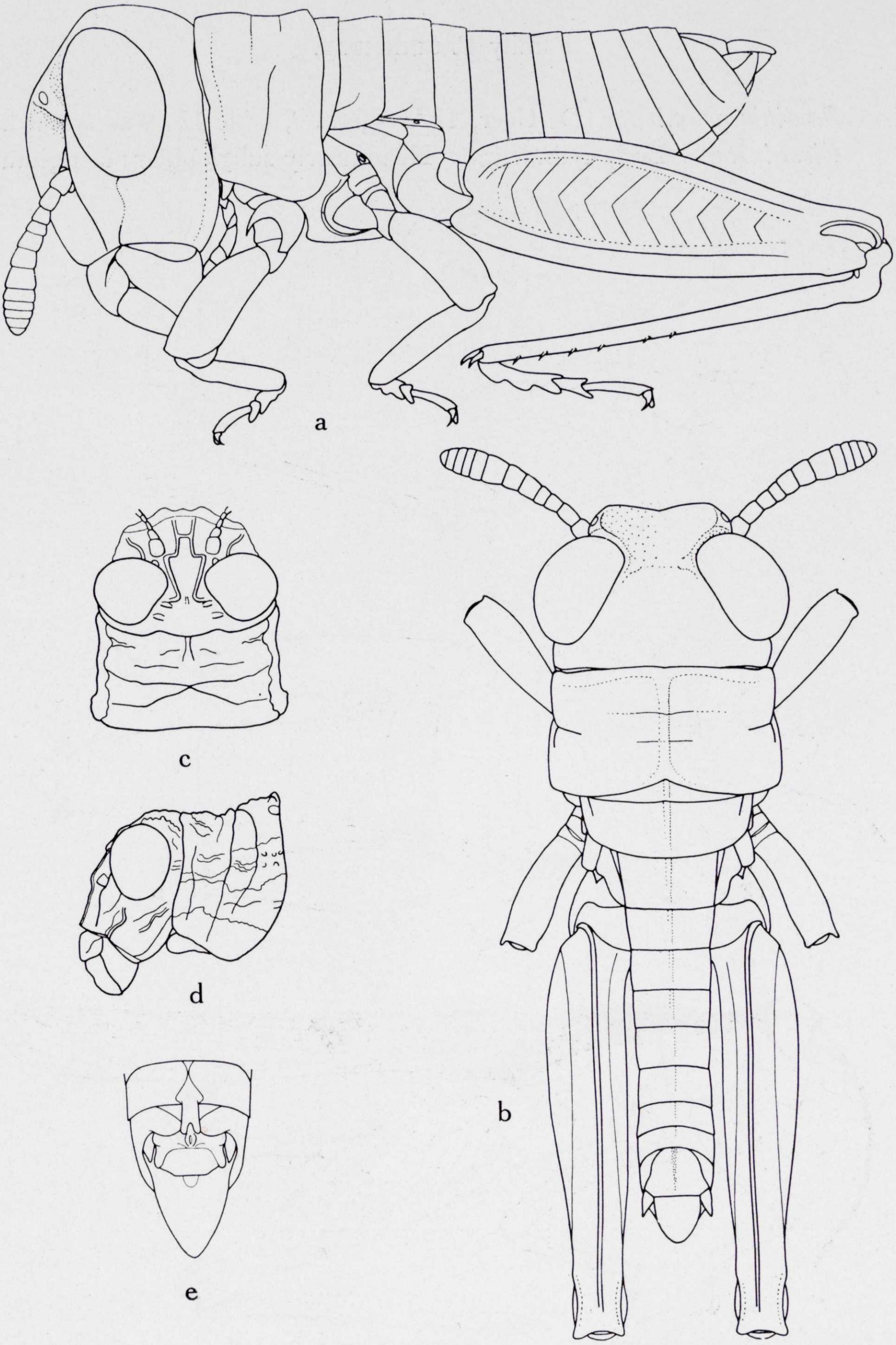

Fig. 38.—*Shelfordites* sp.: *a)* first instar, lateral view; *b)* the same, from above; *c-e)* imago: *c)* head and pronotum from above; *d)* the same, lateral view; *e)* end of abdomen from above.

Family PAULINIIDAE.

Paulinia acuminata (De Geer, 1773) (fig. 39, table 17) was studied. *First instar*. Body cylindrical. Head nearly subglobular; fastigium

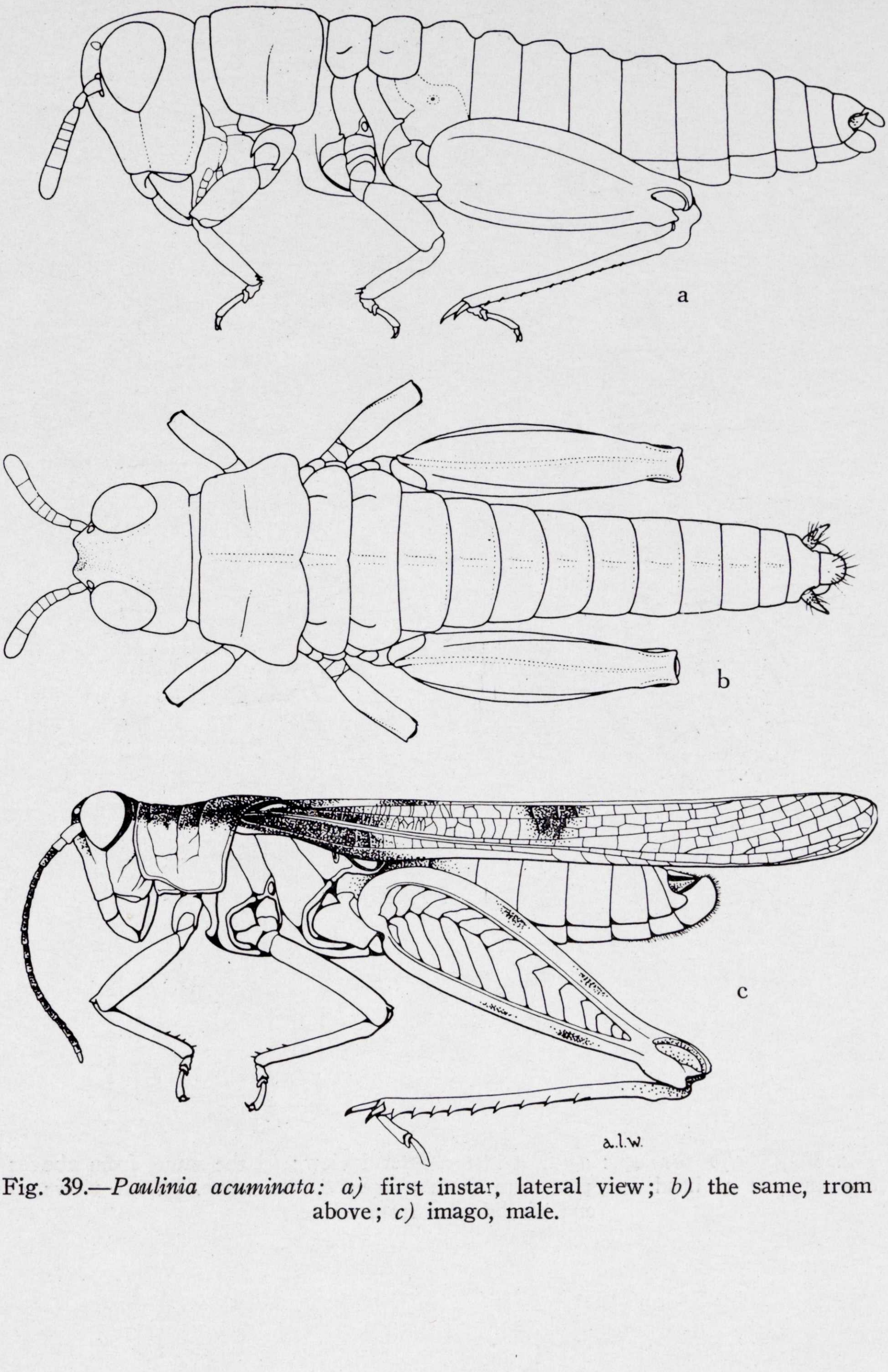

Fig. 39.—*Paulinia acuminata: a)* first instar, lateral view; *b)* the same, from above; *c)* imago, male.

of vertex short, wide, at apex incurved, roundly merging with frons; fastigial furrow absent. Ocelli well developed. Antenna eight-segmented. Pronotum irregularly subcylindrical, its posterior margin incurved in middle. Prosternal process absent. Tympanum detectable. Lower basal lobe of hind femur shorter than upper; whole femur relatively shorter and wider than in imago. Brunner's organ detectable. Hind tibia widened, with spurs and spines specialised as in imago.

Remarkable features in the first instar are the relatively wide and short hind femur, and the lower basal lobe of the femur being shorter than the upper; in all other families studied in this work the lower is mostly longer in this instar. It should be noted also that the structure of the hind tibia is similar to that in the imago.

The specific productivity of linear growth, from the first instar to the imago, is in males 0,991, in females 1,244.

TABLE 17.

Paulinia acuminata.

Instar	Males			Females		
	L	W	Pr	L	W	Pr
I	4,9	1,3	3,8	4,9	1,3	3,8
imago	13,2	3,7	3,6	17,0	4,5	4,8

Family ACRIDIDAE.

Subfamily *Dericorythinae*.

Only *Dericorys cyrtosterna* (Uvarov, 1933) (fig. 40, table 18) was studied.

The number of instars is unknown.

Vermiform larva. Body cylindrical. Head globular, opistognathous, still in embryonic position; fastigium of vertex short, at apex incurved, roundly merging with frons; fastigial furrow absent. Ocelli detectable. Antenna nine-segmented. Cervical ampulla large. Pronotum subcylindrical, without traces of prozonal elevation, its posterior margin straight. Instead of prosternal process, a low transverse convexity. Tympanum detectable. Lower basal lobe of hind femur longer than upper. Brunner's organ faintly detectable. External apical spine of hind tibia present.

First instar. Body cylindrical. Head subglobular, hypognathous;

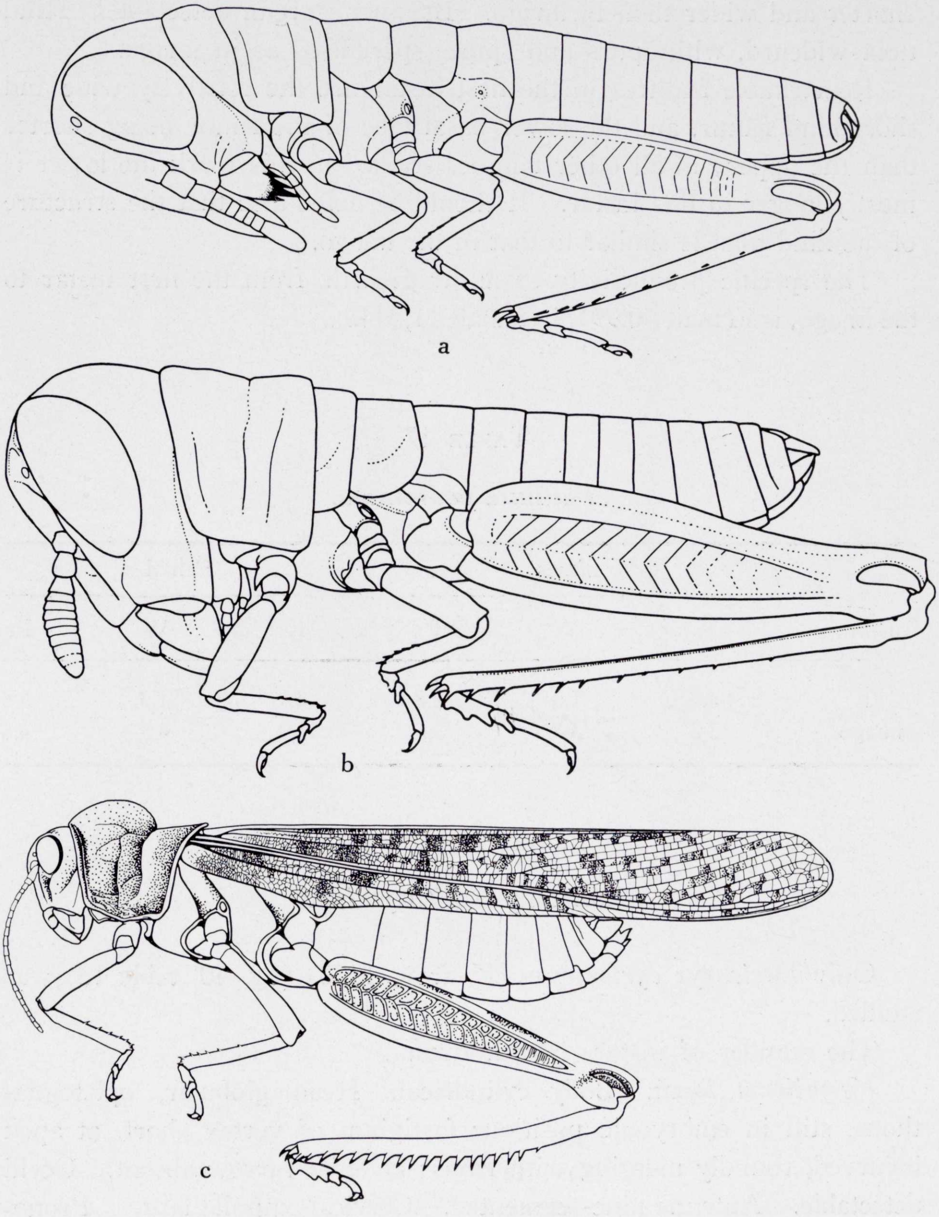

Fig. 40.—*Dericorys cyrtosterna: a)* vermiform larva; *b)* first instar. *Dericorys albidula: c)* imago.

fastigium of vertex short, at apex incurved; fastigial furrow absent. Ocelli readily detectable. Antennae 12-segmented, widened and flattened. Cervical ampulla not visible. Pronotum subcylindrical, its posterior margin straight; no traces of prozonal elevation. Prosternal convexity more pronounced than in first instar. Tympanum hardly detectable. Lower basal lobe of hind femur longer than upper. Brunner's organ detectable. External apical spine of hind tibia present.

The vermiform larva has an embryonic appearance. The first instar differs from the imago, not only in the usual respects, but also in the antennae, which are filiform in the imago, and in the shape of the pronotum, which lacks the dorsal elevation characteristic of the imago in all species of this subfamily.

The specific productivity of linear growth, from the vermiform larva to the imago, is in males 1,480, in females 1,954.

TABLE 18.

Dericorys cyrtosterna.

	Males			Females		
Instar	L	W	Pr	L	W	Pr
Vermiform larva	5,1	1,1	4,6	5,1	1,1	4,6
I	5,2	1,3	4,0	5,2	1,3	4,0
imago	22,4	4,6	4,9	36,0	10,4	3,5

Subfamily *Romaleinae.*

Romalea microptera (Beauvois, 1805) (fig. 41, table 19).

There are five nymphal instars in this species (in addition to the vermiform larva).

Vermiform larva. Body cylindrical. Head globular, opistognathous, in embryonic position; fastigium of vertex short, sloping forwards and roundly merging with frons; fastigial line present. Ocelli traceable. Antenna 11-segmented, compressed, ribbon-like. Pronotum cylindrical, its posterior margin straight. Prosternal process hardly traceable. Tympanum traceable. Lower basal lobe of hind femur slightly longer than upper. Brunner's organ detectable. External apical spine of hind tibia present.

First instar. Body slightly compressed laterally, black with yellowish pattern. Head in normal adult position, subconical, hypognathous; fastigium of vertex short, angular, sloping forwards; fastigial line clearly visible. Ocelli well developed. Antennae 12-segmented, circu-

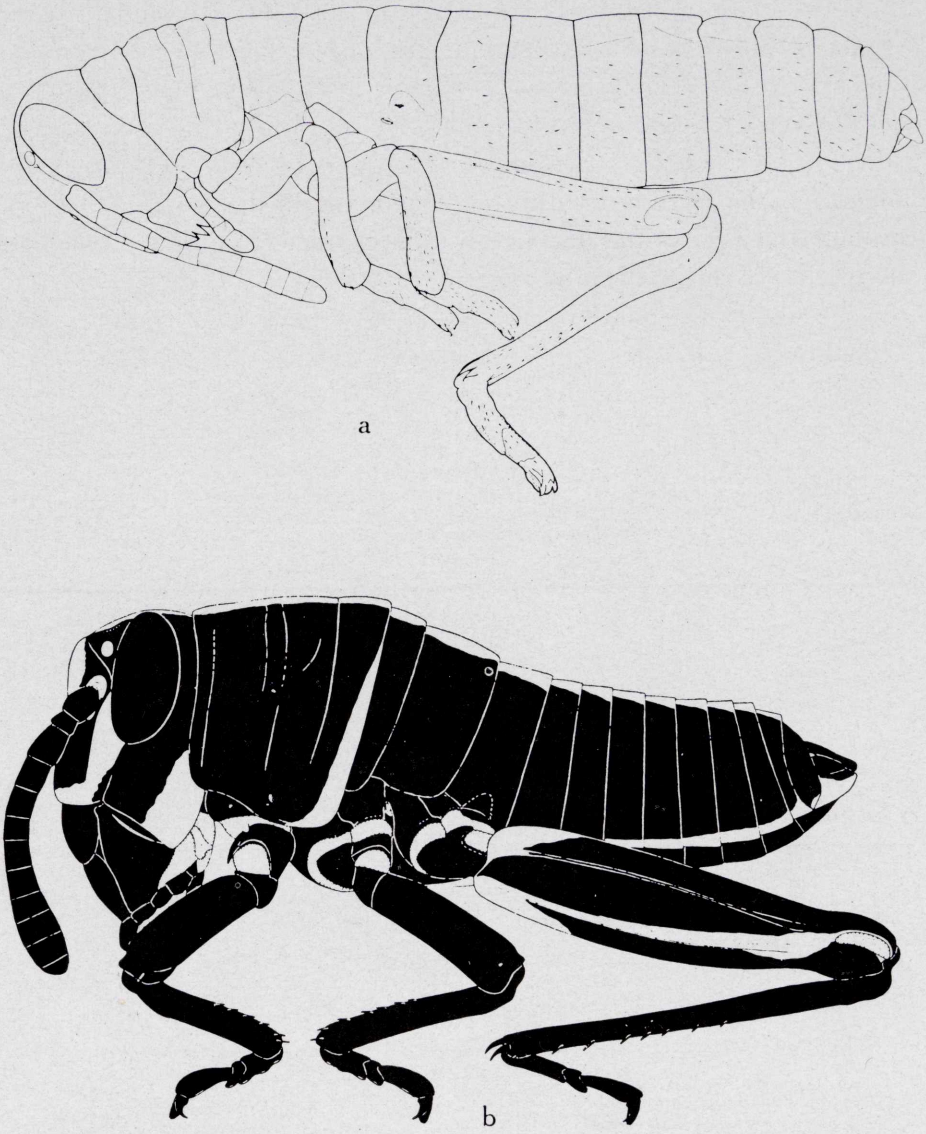

Fig. 41.—*Romalea microptera: a)* vermiform larva; *b)* first instar.

lar in cross-section, widening clubwise apically. Pronotum compressed, tectiform, its posterior margin straight. Prosternal process hardly noticeable. Tympanum detectable. Lower basal lobe of hind femur longer than upper. Brunner's organ traceable. External apical spine of hind tibia present.

It is noteworthy that the shape of the body changes from cylindrical in the vermiform larva to compressed in the first instar, while the head changes from globular to subconical and the antenna from ribbon-like to club-like. There is also a colour change, from vague yellowish to black with yellowish pattern.

In the subsequent instars there are no drastic morphological changes. From being somewhat compressed in the first instar the body gradually becomes subcylindrical as in the imago. The antennae become relatively thinner, losing their club-like widening in the second instar and becoming filiform in the imago. The pronotum becomes less tectiform with every ecdysis, and the prosternal process and the tympanum are more pronounced in every instar. The basal lobes of the hind femur become about equal in length. The posterior margin of the pronotum, however, changes from straight to angular only at the last ecdysis. The coloration and pattern hardly change from the first instar to the imago.

Since the main characters of the subfamily are the peculiar stridulatory mechanism and the internal genitalia which appear only in the imago, the subfamily characters are not conspicuous in the early stages.

The specific productivity of linear growth from the vermiform larva to the imago is in males 1,774, in females 1,946.

TABLE 19.

Romalea microptera.

	Males			Females		
Instar	L	W	Pr	L	W	Pr
Vermiform larva	8,7	2,7	3,2	8,8	2,7	3,3
I	10,4	3,6	2,9	10,4	3,7	2,8
II	13,2	5,0	2,6	13,6	5,0	2,7
III	20,2	7,2	2,8	22,7	7,4	3,1
IV	33,7	8,8	3,8	37,0	10,0	3,7
V	44,2	13,0	3,4	46,7	14,6	3,2
imago	51,3	14,3	3,6	61,6	16,6	3,7

Subfamily *Hemiacridinae*.

Acanthoxia gladiator (Westwood, 1841) (fig. 42, table 20) was studied.

This species is remarkable for the grotesque shape of the head in the imago and the great difference between the nymphs of the earlier instars and the imago. The number of instars is unknown.

Vermiform larva. Body cylindrical. Head subglobular, opistognathous; fastigium of vertex spherically rounded; fastigial furrow absent. Ocelli relatively very large. Antenna 12-segmented, ribbon-like. Cervical ampulla large. Pronotum subcylindrical, its posterior margin slightly incurved. Prosternal process detectable. Basal lobes of hind femur not developed. Brunner's organ detectable. Lobes of hind knee not developed. External apical spine of hind tibia not detectable.

First instar. Body narrow, cylindrical. Integument sparsely hairy. Head subconical, rounded at apex, frons excurved; fastigium of vertex short, angular; fastigial furrow absent. Ocelli well developed. Tympanal organ detectable. Lower basal lobe of hind femur longer than upper. Brunner's organ detectable. Lower outer lobe of hind knee shorter than upper. External apical spine of hind tibia present.

Second instar. Body narrow, cylindrical, relatively narrower than in vermiform larva or first instar, index of proportion being 6,4. Integument much less hairy. Head conical, elongate, with apex rounded, frontal part much longer than in first instar; fastigium of vertex long, angular; fastigial furrow absent. Ocelli well developed. Antennae 13-segmented, club-like, but narrower than in first instar. Tympanum detectable. Lower basal lobe of hind femur shorter than upper. Brunner's organ present. Lower outer lobe of hind knee equal in length to upper. External apical spine of hind tibia present.

In the subsequent instars the body becomes slimmer, the antenna changes gradually to narrow-filiform in the imago, and the head gradually becomes more elongate in the frontal part and finally achieves the grotesque shape of the imago. The upper basal lobe of the hind femur becomes longer with every instar and in the imago is much longer than the lower one, and the lower outer lobe of the hind knee eventually becomes several times longer than the upper. The male subgenital plate grows from instar to instar and most rapidly during the last ecdysis when it reaches its final, very elongate, form and is longer than the pronotum.

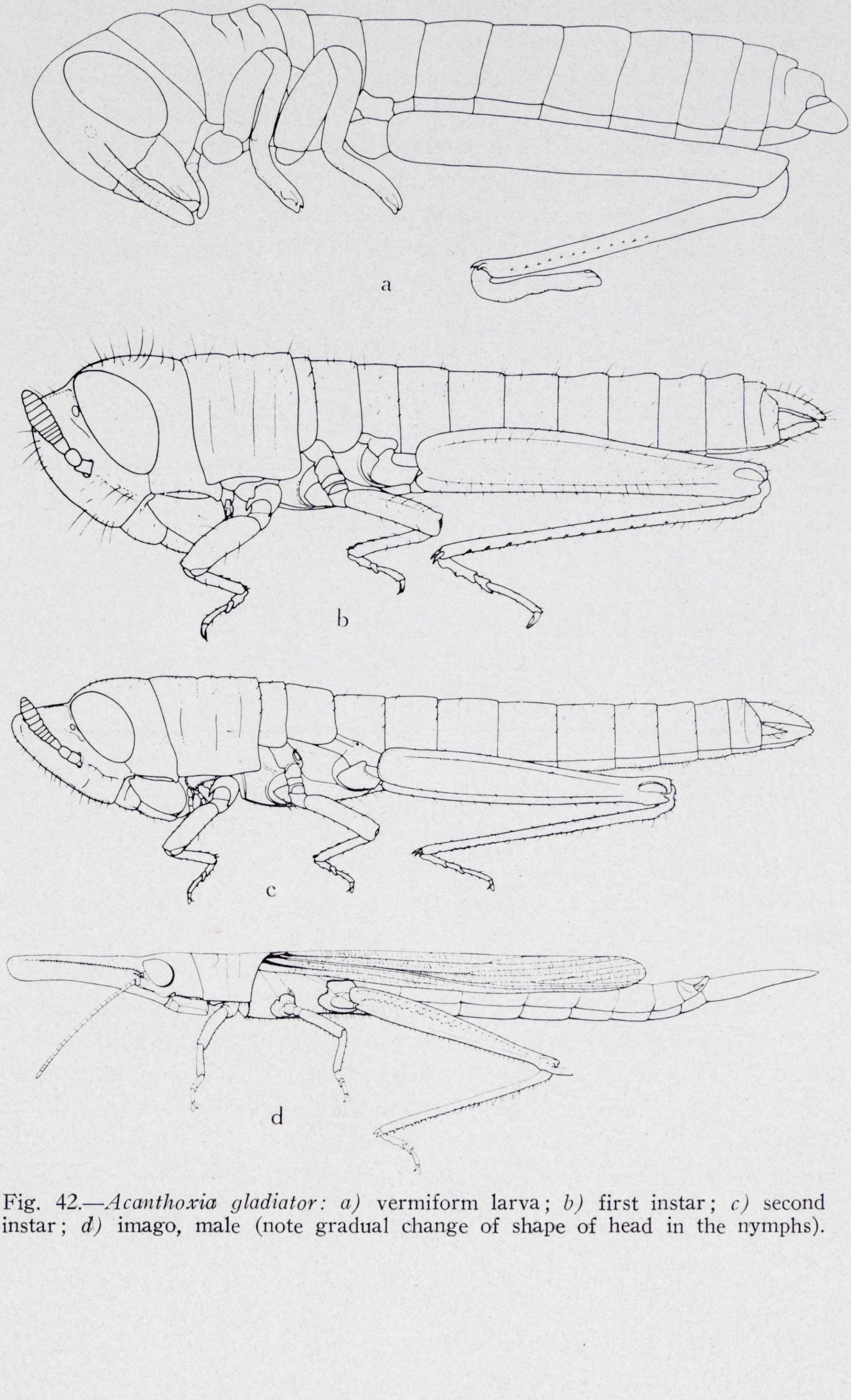

Fig. 42.—*Acanthoxia gladiator: a)* vermiform larva; *b)* first instar; *c)* second instar; *d)* imago, male (note gradual change of shape of head in the nymphs).

The most remarkable feature of the nymphal development of this species is the gradual growth of the frontal part of the head. In other species with elongate heads, in other families and subfamilies (*Cephalocoema, Acrida*), the length of the head as a whole grows rapidly at the first ecdysis and immediately after the ecdysis, and in subsequent instars, it grows approximately proportionally to the body during the whole nymphal period.

The most important features which differentiate this subfamily from others are the peculiar stridulatory mechanism and the structure of the phallic complex, but these occur only in the imago.

The specific productivity of linear growth from the vermiform larva to the imago is in males 2,415, in females 2,697.

TABLE 20.

Acanthoxia gladiator.

	Males			Females		
Instar	L	W	Pr	L	W	Pr
Vermiform larva	6,3	1,3	4,8	6,3	1,3	4,8
I	6,5	1,3	5,0	6,5	1,3	5,0
II	9,6	1,5	6,4	—	—	—
imago	70,5	5,8	12,4	93,5	9,6	9,7

Subfamily *Calliptaminae*.

Caloptenopsis voltaensis (Sjöstedt, 1931) (fig. 43, table 21). This species has five nymphal instars (after the vermiform larva). Its most remarkable feature is that the first moult is performed inside the egg and the first instar emerges leaving the first skin inside the egg shell.

First instar. Body stout, slightly compressed. Integument slightly pigmented in posterior part of body and outer part of hind femur. Head subglobular; fastigium of vertex short, roundly merging with frons; fastigial furrow absent. Ocelli readily traceable. Antennae 13-segmented, thick-filiform. Pronotum tectiform, its posterior margin straight. Prosternal process absent. Tympanum hardly traceable. Lower basal lobe of hind femur as long as upper. Whole femur broad.

Brunner's organ well developed. External apical spine of hind tibia absent. Male cercus simple, narrow-conical.

All the subsequent instars differ from the first in that the antennae become thinner and relatively longer, and the pronotum becomes less

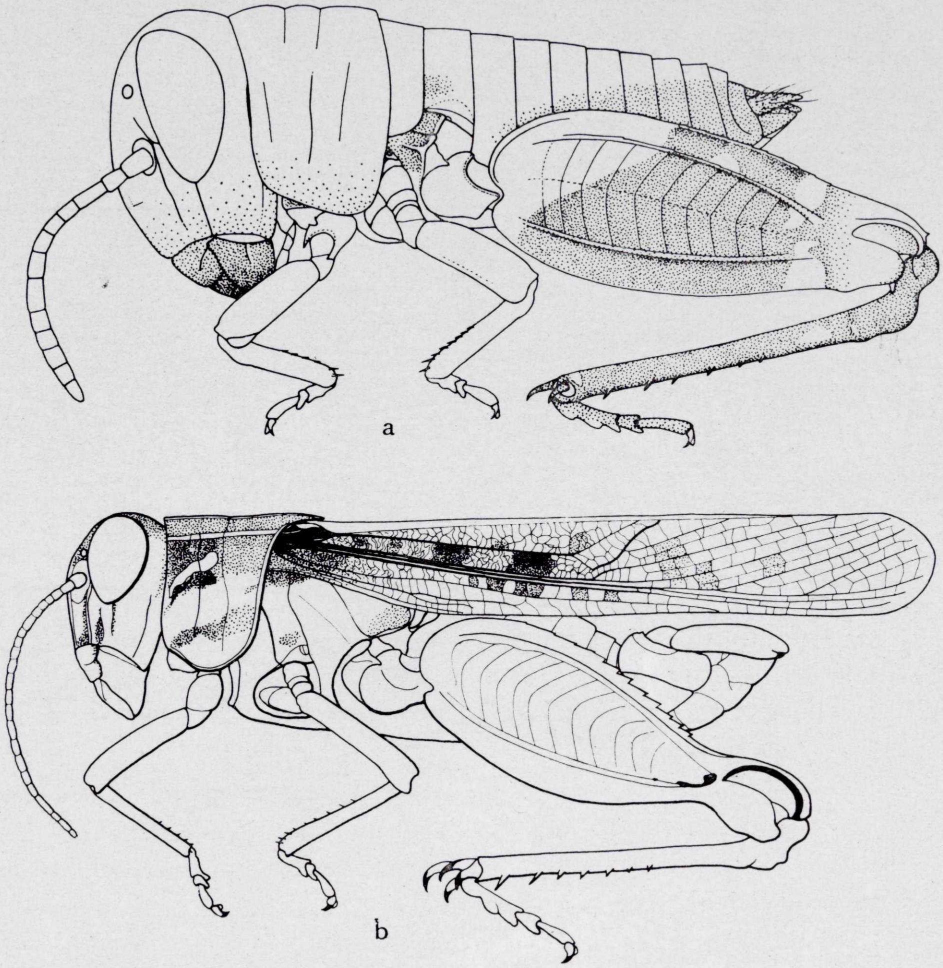

Fig. 43.—*Caloptenopsis voltaensis: a)* first instar; *b)* imago, male.

tectiform from instar to instar until it is almost flat in the imago; its posterior margin becomes excurved in the fourth instar and angularly excurved in the imago. A prosternal process of imago shape appears in the third instar. The male cercus becomes flattened in the third instar and has obtuse apex; in the fourth instar its apex is widely rounded and in the fifth bilobate.

It seems that the two concrete subfamily characters, the shape of the male prosternal process and that of the male cercus, do not appear until the third and fifth instars respectively. The most important subfamily character, the structure of the phallic complex, is developed only in the imago.

The specific productivity of growth, from the vermiform larva to the imago, is in males 1,487, in females 1,935.

TABLE 21.

Caloptenopsis voltaensis.

	Males			Females		
Instar	L	W	Pr	L	W	Pr
Vermiform larva	5,2	1,5	3,5	5,2	1,5	3,5
I	5,4	1,5	3,6	5,4	1,5	3,6
II	9,5	3,6	2,6	9,5	3,6	2,6
III	11,0	3,8	2,9	12,1	4,2	2,9
IV	14,5	4,4	3,3	14,8	4,4	3,4
V	15,1	5,0	3,0	15,4	5,0	3,1
imago	23,0	6,9	3,3	36,0	10,8	3,3

Subfamily *Eyprepocnemidinae*.

Eyprepocnemis plorans meridionalis (Uvarov, 1921) (fig. 44, table 22) was studied.

Antoniou & Hunter-Jones (1951) recorded six, seven and eight nymphal instars in this subspecies in laboratory conditions (excluding the vermiform larva). Jago (1963) claimed that the same subspecies (reared in the same laboratory) has two types of cycle of development, one in which both sexes have a seven-instar nymphal cycle and another in which the female has an eight-instar cycle (again excluding the vermiform larva). The material studied in the present investigation represented the seven-instar nymphal cycle.

Vermiform larva. Body cylindrical. Head in front globular, opistognathous; fastigium of vertex short, roundly merging with frons; fastigial line faintly indicated. Ocelli hardly detectable. Antenna rod-like, ten-segmented. Cervical ampulla large. Pronotum subcylindrical, its posterior margin slightly incurved. Prosternal process not detectable. Basal lobes of hind femur not developed. Lobes of hind knee not developed. Brunner's organ traceable. External apical spine of hind tibia absent. Supra-anal plate and cerci in embryonic position.

First instar. Body slightly compressed laterally. Head subglobu-

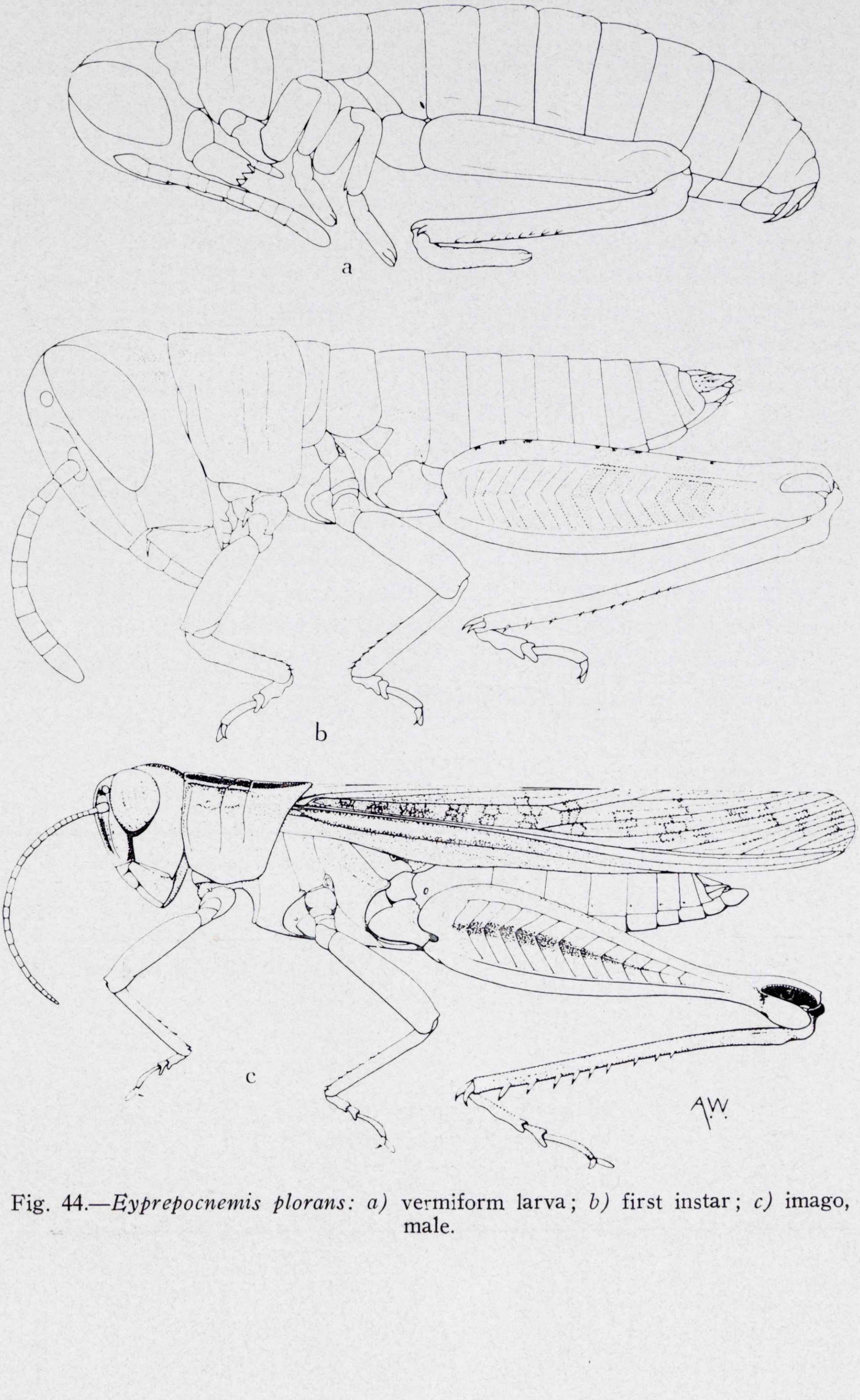

Fig. 44.—*Eyprepocnemis plorans: a)* vermiform larva; *b)* first instar; *c)* imago, male.

lar; fastigium of vertex short, sloping forwards; fastigial line hardly detectable. Ocelli well developed. Antenna slightly widened in apical part. Pronotum tectiform; posterior margin of metazona slightly incurved. Prosternal process hardly detectable. Tympanum traceable. Lower basal lobe of hind femur slightly longer than upper. Brunner's organ well developed. External apical spine of hind tibia absent. Male cercus acutely conical, straight. Traces of pigmentation present on postocular area of head, pronotum and outer side of hind femur.

In subsequent instars, beginning at the second, the body becomes cylindrical, the head becomes relatively smaller in every instar, and the antenna becomes narrower and fully filiform and there is an increase in the number of antennal segments (table 2). The pronotum is subcylindrical in the second instar, and not until the fourth instar does its dorsum flatten. The prosternal process in the third instar is small and pyramidal, in the fourth instar obtusely conical and in the fifth cylindrical. The tympanum in the second instar is readily visible and in the third well developed. The basal lobes of the hind femur are of equal length in the third instar, and in the fourth the lower lobe becomes shorter than the upper. The male cercus in the first three instars is conical, but in the fourth it is already flattened and slightly downcurved. The characteristic pattern of the pronotum appears in the third instar and the posterior margin of the metazona is excurved in the fifth.

The specific productivity of linear growth, from the vermiform larva to the imago, is in males 1,826, in females 2,125.

TABLE 22.

Eyprepocnemis plorans meridionalis.

	Males			Females		
Instar	L	W	Pr	L	W	Pr
Vermiform larva	4,8	1,4	3,4	4,8	1,4	3,4
I	5,0	1,7	2,9	5,0	1,7	2,9
II	9,0	2,2	4,1	9,0	2,2	4,1
III	11,6	2,8	4,1	12,7	3,0	4,2
IV	15,2	3,6	4,2	18,0	4,6	3,9
V	22,5	5,0	4,5	25,0	5,8	4,3
VI	26,0	6,0	4,3	31,8	7,0	4,5
VII	28,6	6,4	4,5	35,0	7,8	4,5
imago	29,8	6,4	4,4	40,2	7,9	5,1

Subfamily *Cyrtacanthacridinae*.

Schistocerca gregaria gregaria (Forskål, 1775) (table 23).

The material of this subspecies studied was considered to be intermediate between gregarious and solitarious. There are usually five nymphal instars (after the vermiform larva), but the number varies with the rearing conditions.

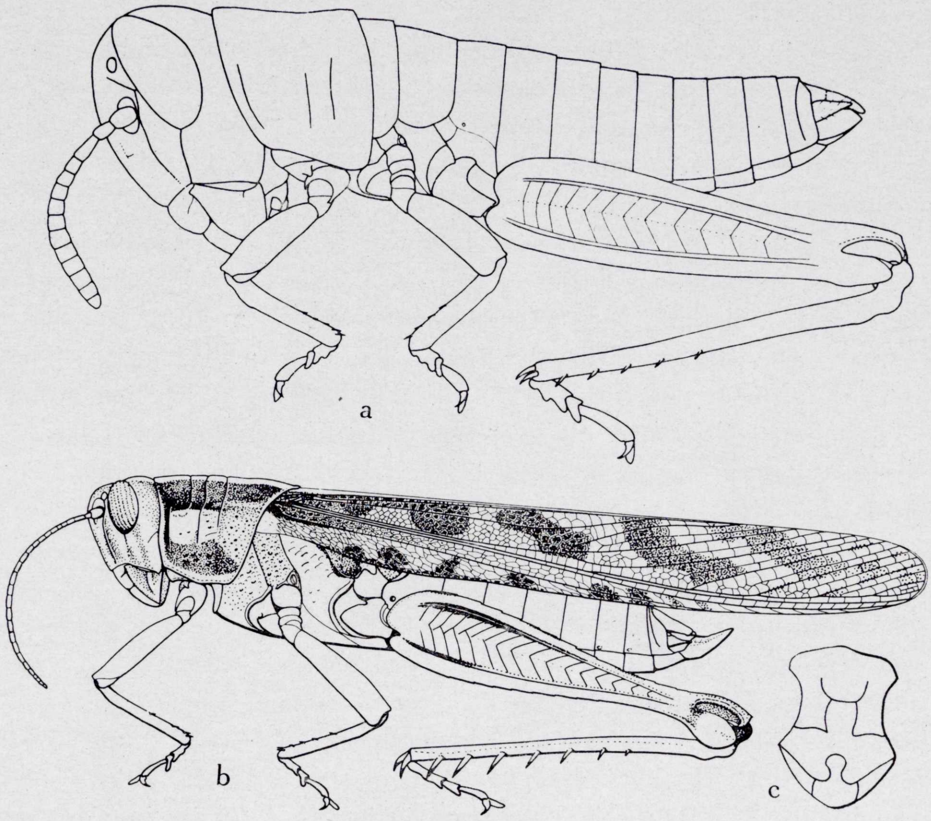

Fig. 45.—*Cyrtacanthacris tatarica: a)* first instar; *b)* imago, male; *c)* meso- and metasternum.

Vermiform larva. Body cylindrical. Head and appendages in usual embryonic position. Head subglobular with rounded apex; fastigium of vertex short, sloping forwards; fastigial line hardly detectable. Ocelli well detectable. Antennae 13-segmented, ribbon-like. Cervical ampulla large. Pronotum subcylindrical, its posterior margin incurved. Prosternal process not detectable. Mesosternal lobes narrow-elongate with margins not clearly defined. Tympanum traceable. Lower basal lobe of hind femur slightly longer than upper. Brunner's organ detectable. External apical spine of hind tibia absent. Male cercus conical, in embryonic position.

First instar. Body slightly compressed. Head subglobular, in normal adult position; fastigium of vertex short, roundly merging with frons; fastigial line hardly detectable. Ocelli well developed. Antenna 13-segmented, thick, slightly widened apically. Pronotum slightly compressed, its posterior margin incurved. Prosternal process not detectable. Tympanum traceable. Lower basal lobe of hind femur slightly longer than upper. Brunner's organ clearly detectable. Male cercus conical, straight.

Development of the subsequent instars is as follows. In the second instar the body returns to the subcylindrical shape, which continues to the imago. The head becomes relatively smaller from instar to instar, but from the second instar its shape undergoes only small changes. The antenna in the second instar is filiform and in every succeeding instar becomes relatively thinner and increases in number of segments (table 2). The pronotum in the second instar is less compressed, and the prosternal process appears. The mesosternal lobes acquire a rectangular form. The tympanal organ is more developed. The lower and upper basal lobes of the hind femur are of equal length in the second instar and in subsequent instars the upper lobes become longer. Brunner's organ is well developed. The male subgenital plate acquires a deep apical incision in the second instar, and the male cercus remains angular up to the fourth instar but then flattens and widens apically.

The body proportion index *(Pr)* changes very little during the whole nymphal period. The volume and weight increase steadily from instar to instar, but not so regularly as to be expressed by a simple mathematical formula.

The specific productivity of linear growth, from the vermiform larva to the imago, is in males 1,744, in females 1,864.

The same pattern of development was observed in *Cyrtacanthacris tatarica tatarica* L. (fig. 45) and *Nomadacris septemfasciata* Serv., except that the number of nymphal instars in the former is five or six and in the latter six or seven.

TABLE 23.

Schistocerca gregaria.

	Male					Female				
Instar	L	W	Pr	Volume in mm^3	Weight in gm	L	W	Pr	Volume in mm^3	Weight in gm
Vermiform larva	8,9	2,1	4,2	13,5	0,020	8,9	2,1	4,2	13,5	0,020
I	10,3	2,4	4,3	15,6	0,036	10,2	2,4	4,3	16,9	0,039
II	17,2	3,9	4,4	120,5	0.057	17,8	4,0	4,5	125,0	0,077
III	25,1	5,0	5,0	300,0	0,129	25,5	5,2	4,9	326,1	0,141
IV	30,2	7,0	4,3	606,1	0,306	31,6	7,4	4,3	740,1	0,341
V	45,9	10,0	4,6	833,3	0,865	50,5	10,2	5,0	2142,9	1,013
imago	50,9	11,0	4,6	3325,0	1,368	57,4	12,5	4,6	4098,0	1,770

Subfamily *Acridinae*.

Acrida bicolor (Thunberg, 1815) (fig. 46, table 24).

The number of nymphal instars varies; it depends upon the ecological conditions and is related to the final size of the body in adults, larger specimens having more instars. The body size (length) in the imago varies over a wide range (male 31-53, female 51-80 mm). In the population studied (from Mali) the males had six and the females seven nymphal instars.

Vermiform larva. Body cylindrical. All appendages in embryonic position. Head short, with apex widely rounded. Fastigium of vertex almost non-existent, apex of head in front of eyes roundly merging with frons; however, some folds on apical part of frons suggest that the whole fastigium is folded like a concertina and the growth of it between the vermiform larva and the first instar is mostly an unfolding of the cuticle and only partly actual growth (fig. 46). Fastigial line faint. Ocelli not detectable. Antenna ribbon-like, narrow. Pronotum cylindrical, its posterior margin incurved. Trace of tympanum detectable. Hind femur short, slightly shorter than half length of abdomen, ratio of length to width 5,3; basal lobes poorly defined but lower part protrudes more than upper. Brunner's organ hardly detectable. External apical spine of hind tibia absent. Cercus conical and supra-anal plate elongate angular; both in embryonic position.

A most remarkable feature of the vermiform larva is the rapid growth and change of shape of the head, which can be observed in the space of a few minutes. When a vermiform larva emerges from the soil it has the appearance shown in fig. 46 (a); then the head begins to grow and in a few minutes the ecdysial line ruptures and when the cuticle of the head is shed the head already has the appearance shown in fig. 46 (b).

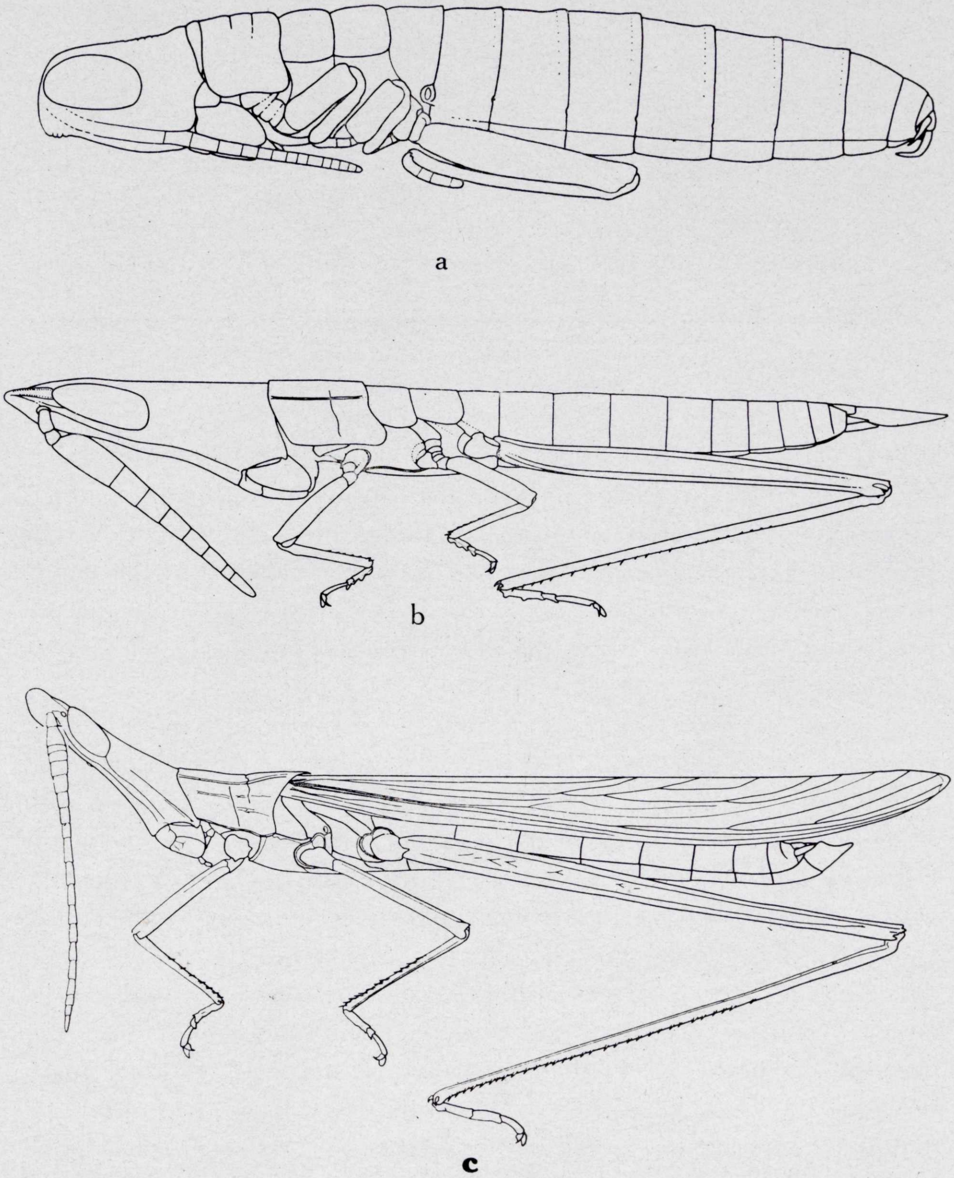

Fig. 46.—*Acrida bicolor: a)* vermiform larva; *b)* first instar; *c)* imago, male (note change in shape of head).

First instar. Body elongate, narrow-cylindrical. All appendages in normal imago position, embryonic positions being lost entirely. Head very elongate, narrow, acutely conical; fastigium of vertex elongate, angular, projecting far in front of eyes; fastigial line hardly detectable. Ocelli detectable. Antenna ensiform, of imago shape. Pronotum subcylindrical, its posterior margin slightly incurved. Hind femur very elongate, about as long as abdomen, narrow, ratio of length to width 12,2; basal lobes of femur well developed; lower lobe shorter than upper. Brunner's organ clearly detectable. Cercus acutely conical, straight. Supra-anal plate very elongate, narrow, acutely angular.

The main features of the first instar in comparison with the vermiform larva are the striking changes in the shape and proportions of the head, antenna and hind femur and the disappearance of the embryonic features of the abdominal appendages.

The subsequent instars display small changes in proportion (table 24) at each ecdysis up to the last, when the wings grow rapidly and the external genitalia acquire the adult form. The most remarkable change is in the supra-anal plate (fig. 22). In all nymphal instars and the vermiform larva it is very elongate, narrow and angular, but during the last ecdysis it is reduced to the normal short imago form.

The specific productivity of linear growth, from the vermiform larva to the imago, is in males 1,716, in females 2,178.

TABLE 24.

Acrida bicolor.

	Males			Females		
Instar	L	W	Pr	L	W	Pr
Vermiform larva	8,0	1,3	6,1	8,0	1,3	6,1
I	11,2	1,4	8,0	11,4	1,4	8,1
II	16,5	1,6	10,3	17,0	1,7	10,0
III	19,6	2,0	9,8	21,4	2,3	9,3
IV	27,0	2,3	11,3	28,6	3,1	9,2
V	32,5	2,7	12,0	33,2	3,8	8,7
VI	41,3	4,5	9,2	43,6	4,8	9,1
VII	—	-	—	65,0	6,7	9,7
imago	44,5	5,5	8,1	70,6	9,2	7,8

Gastrimargus procerus (Gerstaecker, 1889) (fig. 47, table 25).

This species has five nymphal instars in both sexes in the population investigated. According to Descamps, 1961, males have 5 and females 6 instars. The vermiform larva was not available.

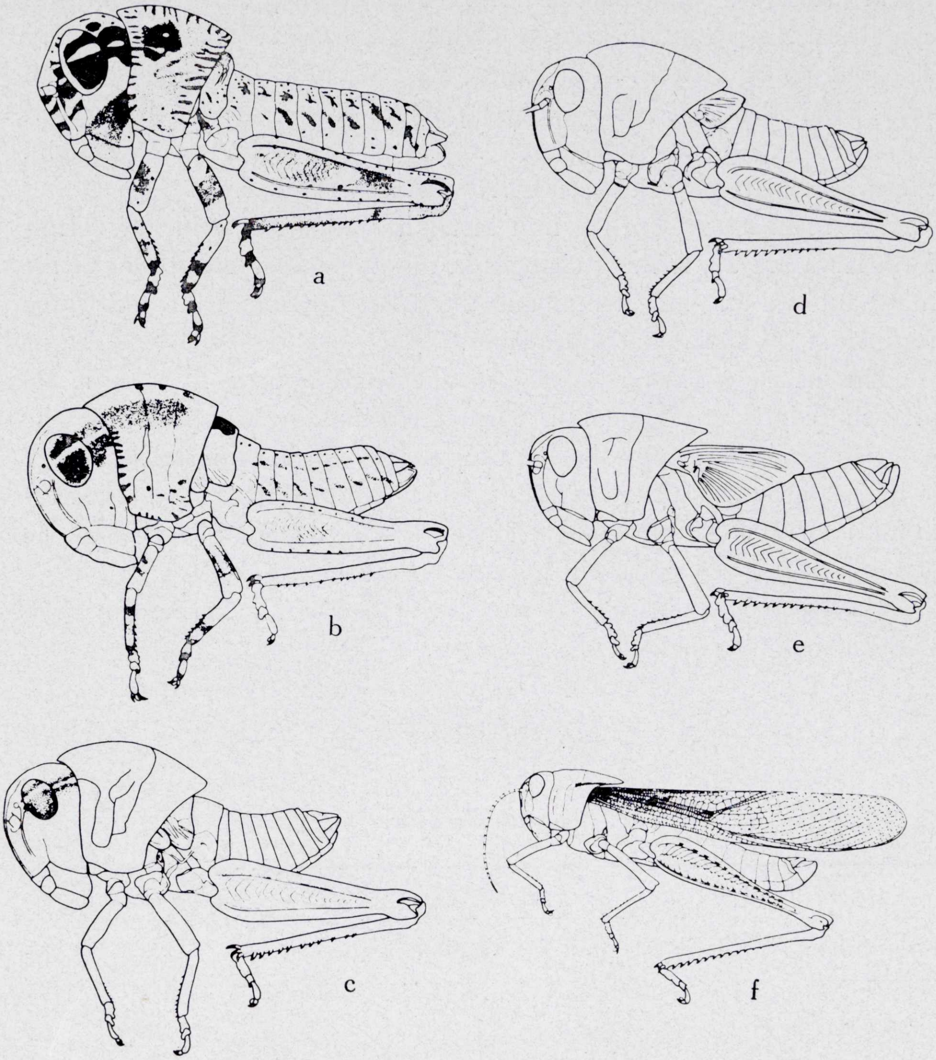

Fig. 47.—*Gastrimargus procerus: a-e)* first to fifth instars, respectively; *f)* imago, male.

First instar. Body slightly compressed laterally. All appendages of body in imago position. Head subglobular; fastigium of vertex strongly sloping forwards and obtuse-angularly merging with frons; fastigial line hardly noticeable. Ocelli readily detectable. Antenna filiform, 13-14-segmented. Pronotum tectiform, its posterior margin obtuse-angularly excurved; in upper, lateral part of pronotum a hemispherical, shiny, black tubercle. Tympanum traceable. Basal lobes of hind femur of equal length. Brunner's organ detectable. External apical spine of hind tibia absent. Integument strongly pigmented, with definite pattern.

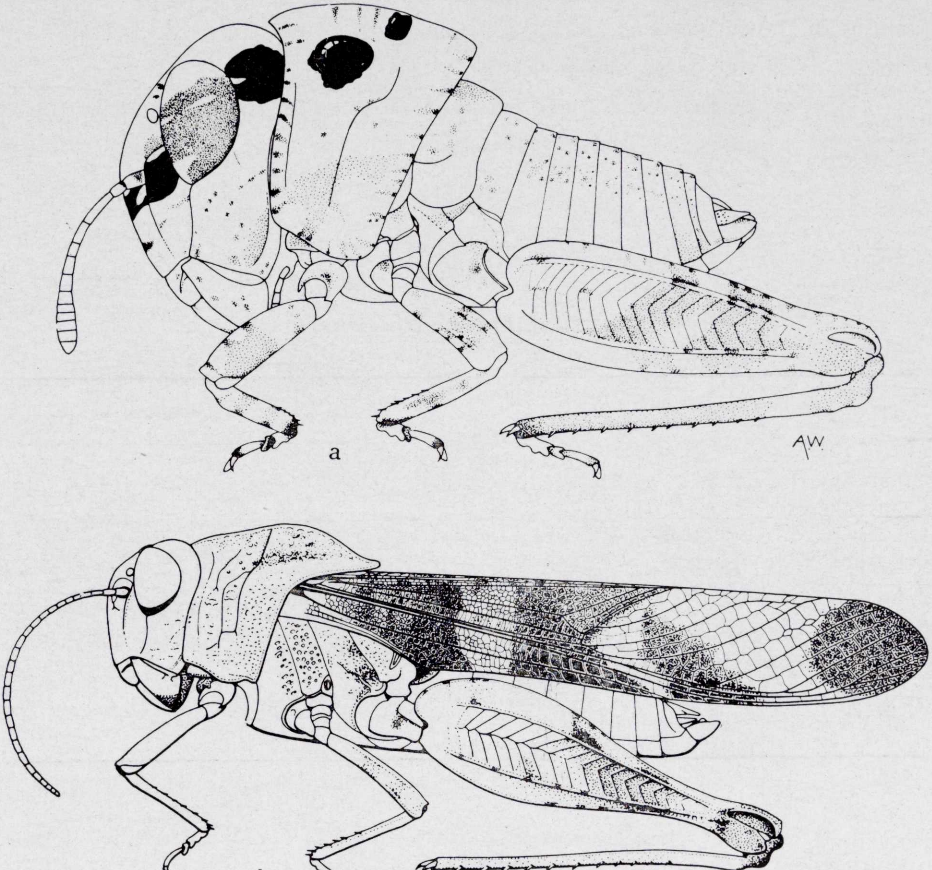

Fig. 48.—*Humbe tenuicornis: a)* first instar; *b)* imago, male.

The subsequent instars differ from the first as follows. In the second instar the head becomes more globular, the tubercle on the side of the pronotum disappears, the integument becomes less pigmented and the tympanum is more developed. The third instar differs in that the pattern has disappeared from the body, but is still present on the head, that the lower lobe of the hind femur is now shorter than the upper and that the tympanum is well defined. In the fourth and fifth instars the pattern of the integument is absent completely.

The most interesting feature of the development of this species is the glassy tubercle on the side of the pronotum in the first instar, which disappears in the second. The gradual diminishing of the pattern of the integument seems also unusual.

A lateral tubercle on the pronotum similar to that of this species occurs in the first instar of *Humbe tenuicornis* (Schaum, 1853) (fig. 48). *Humbe* is in the same group of genera as *Gastrimargus*.

The specific productivity of linear growth, from the first instar to the imago, is in males 1,642, in females 1,771.

TABLE 25.

Gastrimargus procerus.

	Males			Females		
Instar	L	W	Pr	L	W	Pr
I	6,0	2,1	2,9	8,0	2,8	2,9
II	8,5	3,2	2,7	9,5	3,5	2,7
III	12,0	5,1	2,4	15,5	6,8	2,3
IV	16,7	6,1	2,7	24,5	8,8	2,8
V	23,0	5,9	3,9	29,1	8,3	3,5
imago	31,0	8,6	3,6	47,0	12,8	3,7

Locusta migratoria migratorioides (Reiche & Fairmaire, 1850) (fig. 49, table 26).

The number of nymphal instars (after the vermiform larva) in this subspecies has been variously recorded as five or six for both sexes or five for males and six for females. It is probably related to environmental conditions, size of insects, or some hereditary factor. A population with five nymphal instars in both sexes was investigated; it was intermediate in form between gregarious and solitarious.

Vermiform larva. Body cylindrical. All appendages in embryonic position. Head in profile parabolic, opistognathous; fastigium of vertex roundly merging with frons; fastigial line hardly noticeable. Ocelli well developed. Antenna 13-segmented, ribbon-like. Pronotum cylindrical, its posterior margin slightly incurved. Tympanum not detectable. Lower basal lobe of hind femur longer than upper. Brunner's organ faintly detectable. External apical spine of hind tibia absent.

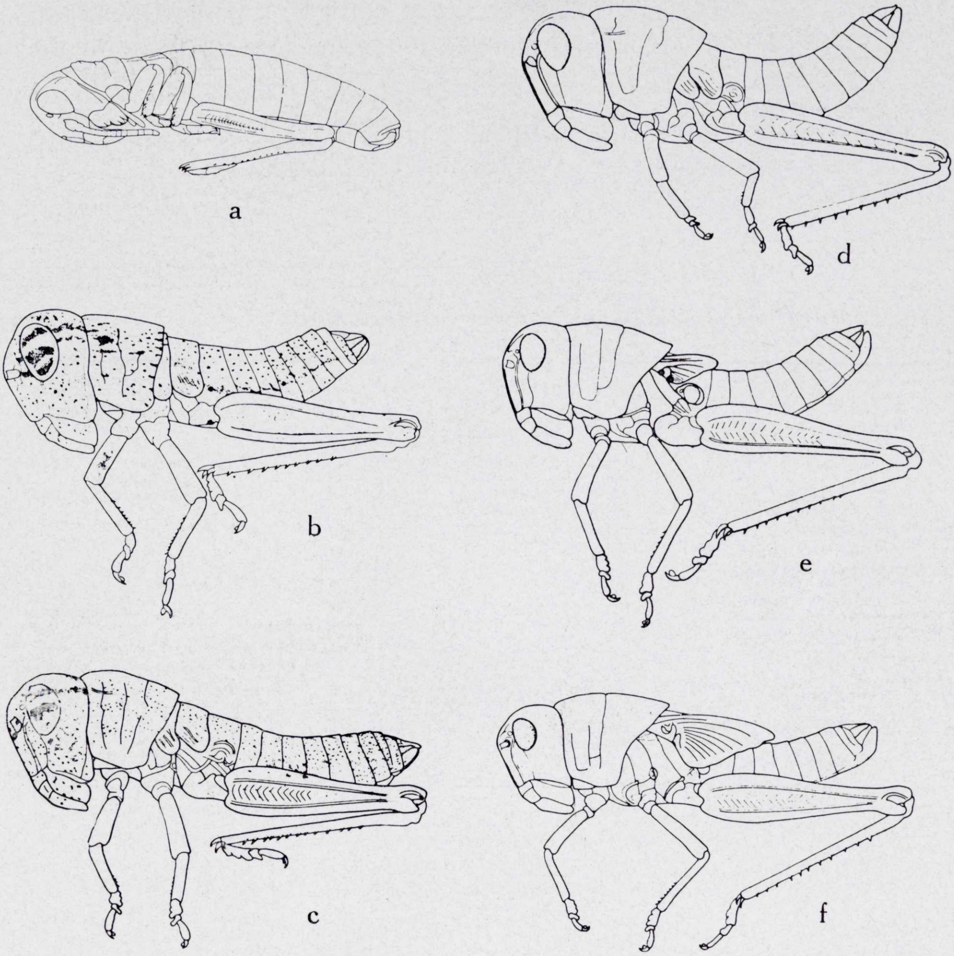

Fig. 49.—*Locusta migratoria migratorioides: a)* vermiform larva; *b-f)* first to fifth instars, respectively.

Cercus and supra-anal plate in embryonic position. No pigmentation of integument noticeable.

First instar. Body slightly compressed laterally. All body appendages in normal imago position. Head subglobular, in normal, hypognathous, imago position; fastigium of vertex sloping forwards; fastigial line hardly noticeable. Ocelli well developed. Antenna filiform. Pronotum tectiform, its posterior margin straight. Tympanum detectable. Lower basal lobe of hind femur as long as upper. Brunner's organ detectable. External apical spine of hind tibia absent. Cerci and supra-anal plate in normal adult position. Pigmentation of integument apparent (fig. 49).

All subsequent instars follow the usual pattern of nymphal development without any spectacular changes. The lower basal lobe of the hind femur becomes shorter than the upper in the third instar.

The specific productivity of linear growth from the vermiform larva to the imago is in males 1,651, in females 1,817.

TABLE 26.

Locusta migratoria migratorioides.

	Males					Females				
Instar	L	W	Pr	Volume in mm³	Weight in mg	L	W	Pr	Volume in mm³	Weight in mg
Vermiform larva	7,1	1,4	5,1	16,1	14	7,1	1,4	5,1	16,1	14
I	8,3	2,3	3,6	29,3	14	8,4	2,3	3,7	28,4	14
II	15,5	4,1	3,8	95,7	33	15,5	4,1	3,8	100,0	38
III	19,2	5,8	3,3	192,2	72	19,9	5,9	3,4	220,6	77
IV	26,1	7,8	3,3	429,6	174	27,1	7,9	3,4	500,0	208
V	34,1	9,6	3,6	1000,0	409	36,4	10,0	3,6	1215,4	487
imago	37,0	9,7	3,8	2600,0	904	43,7	11,8	3,7	6000,0	1251

Subfamily *Truxalinae*.

Mesopsis gracilicornis (Krauss, 1877) (fig. 50, table 27).

In the population studied there were five instars (after the vermiform larva) in both sexes.

Vermiform larva. Body elongate-cylindrical. Head conical, with apex obtuse; fastigium of vertex parabolic, shorter than length of eye; fastigial line faint. Ocelli not detectable. Antenna narrow, flattened, ribbon-like. Pronotum cylindrical, its posterior margin incurved. Prosternal process not noticeable. Mesosternal interspace closed. Tympanum not detectable. Lower basal lobe of hind femur as long as upper. Brunner's organ hardly detectable. External apical spine of hind tibia absent. Supra-anal plate very elongate, narrow, folded backwards below abdomen (in the embryonic position). Cercus long, narrow, conical, also folded backwards.

First instar. Body narrow-cylindrical. Head conical with apex obtuse; fastigium of vertex narrow, one-and-a-half times as long as eye; fastigial line detectable. Ocelli detectable. Antenna ensiform. Pronotum cylindrical, its posterior margin straight. Prosternal process noticeable. Tympanum faintly detectable. Brunner's organ detectable.

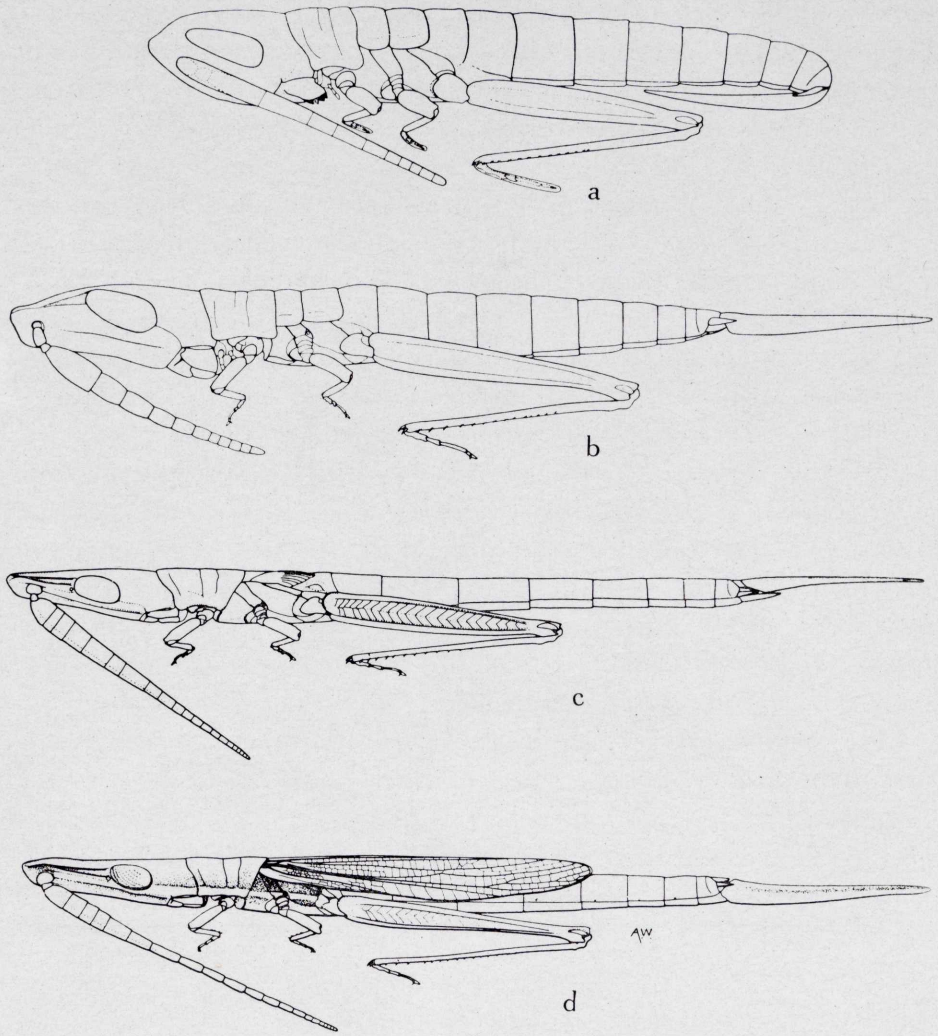

Fig. 50.—*Mesopsis gracilicornis: a)* vermiform larva; *b)* first instar; *c)* penultimate instar; *d)* imago, male.

Rudimentary stridulatory tubercles on inner side of hind femur, forming irregular row. Supra-anal plate and cerci unfolded and in normal position.

In each of the following instars the head becomes longer and relatively narrow, the fastigium of the vertex becomes relatively longer and narrower, the ocelli more developed, the antenna longer and wider. The pronotum grows relatively little, but its posterior margin in the fifth instar becomes excurved. The tympanum develops progressively from instar to instar and the stridulatory serration on the inner side of the hind femur grows gradually and acquires a regular linear order in the last instar. The supra-anal plate remains very elongate through all the nymphal instars and only at the last ecdysis is it reduced in both sexes to the short, angular shape of the imago. Another phenomenon which occurs at the last ecdysis is that the male subgenital plate grows abruptly to a remarkable length, becoming in the adult as long as or longer than the supra-anal plate in the last nymphal instar.

The most noteworthy features of the development of this species are the great but gradual growth and reshaping of the head; the reduction of the supra-anal plate and the rapid growth of the male subgenital plate at the last ecdysis; and the appearance of the stridulatory serration on the hind femur in the first instar. In the genera *Truxalis* and *Truxaloides* also rudiments of the stridulatory serration were found in the first instar, and Roscow (1963) recorded the same phenomenon in the same instar in *Stenobothrus lineatus* (Panzer, 1796).

The specific productivity of linear growth, from the vermiform larva to the imago, is in males 1,682, in females 2,155.

TABLE 27.

Mesopsis gracilicornis.

	Males			Females		
Instar	L	W	Pr	L	W	Pr
Vermiform larva	8,0	1,2	6,6	8,0	1,2	6,6
I	9,5	1,1	8,6	9,5	1,1	8,6
II	12,2	1,2	10,2	12,4	1,2	10,3
III	14,3	1,4	10,2	15,4	1,4	11,0
IV	22,2	1,6	13,9	25,0	1,8	13,9
V	26,0	1,8	14,4	28,4	2,0	14,2
imago	43,0	4,0	10,8	69,0	6,0	11,5

CONCLUSIONS.

The aim of this paper is not only to describe the post-embryonic development of *Acridomorpha,* but also to find indications of the phylogenetic relationships between the various groups of *Acridomorpha* on the basis of their ontogeny.

The background of this research is most precarious. Palaeontological data concerning *Acridomorpha* are almost non-existent. A few *Eumastacidae* or alleged *Eumastacidae* have been found in the Oligocene and Miocene systems (Cockerell, 1909, 1926; Tillyard, 1922; Zeuner, 1941, 1942, 1944). One specimen of *Pyrgomorphidae* has been found in the Upper Miocene, Sarmatian (Kevan, 1965), and some recent genera —*Podismopsis, Stenobothrus, Chorthippus* and *Gomphocerus*— in the Pleistocene (Zeuner, 1942). Thus there is very little possibility of our being able to rely on palaeontological data, and we must try to make some tentative conclusions based on comparative morphology.

The first problem is whether or not to accept Haeckel's (1866) "biogenetic law" that ontogeny repeats phylogeny. The majority of scientists at present, particularly the neodarkinists (De Beer, 1958), reject it completely. Some authors, however, while not accepting it in full, are of the opinion that ontogeny in certain respects may reflect the phylogeny of the group, and many accept it with much reservation and amendment (Spett, 1957; Sharov, 1958). However, in the opinion of the present writer the biogenetic law of Haeckel cannot be rejected fully and uncompromisingly; there are too many facts and indications which prevent its being ignored.

The main difficulty is to decide which of the characters that are now in general use for the differentiation of taxa are the more primitive. Since there are no adequate palaeontological data conjecture and logical deduction must be employed in assessing each character in this respect. It should be borne in mind that the term primitive means ancestral, not merely simple or simplified.

Unfortunately only the external morphological characters can be used for this purpose, as the development internal characters during post-embryonic ontogeny is still almost unknown. A particular need is a study of the development of the phallic complex, which alone can serve as a diagnostic character for superfamilies, families, subfamilies and even genera and in many cases species, in the imago stage.

It has been observed and generally assumed, and in many cases proved, that the more primitive insects are, the fewer are the morphological changes that occur in their post-embryonic development. A good example is provided by the whole subclass *Apterygota;* they are primarily wingless, and have from six to sixty ecdyses, in the course of which they change little except in size; some of them have ecdyses in the imago stage as well.

In the *Eumastacidae,* in the only representative studied, *Keyacris scurra* of the subfamily *Morabinae,* it was observed that the changes during the postembryonic period are negligible, even the number of antennal segments remaining unchanged from the vermiform larva to the imago. The only changes which can be observed are the development of the external sexual appendages in both sexes and the increase in size and slight changes in proportions. This lack of morphological differentiation is analogous to that of the *Apterygota* and may be considered as a primitive character indicating a primitiveness in the group. The possibility that it may merely be a secondary simplification indicating degeneration of the group must not be overlooked, but a study of the whole suborder *Acridomorpha* strongly indicates that it is a primitive and not a degenerative feature. To support this point of view there are the examples of many genera of the family *Lentulidae* which in the imago stage manifest a highly simplified, nymphal appearance of the bodies, suggesting neoteny or degeneration rather than primitiveness.

There is another example in the superfamily *Eumastacoidea,* namely *Cephalocoema canaliculata* of *Proscopiidae.* In its development it almost repeats the development of *Keyacris scurra,* the difference being that the number of antennal segments increases from eight in the vermiform larva to ten in the imago. However, the species has a feature which is absent in other *Acridomorpha,* in that its phallic complex is not fully bilaterally symmetrical (Dirsh, 1956). All other *Acridomorpha* studied have the phallic complex bilaterally symmetrical. An asymmetrical phallic complex is found in all *Dictyoptera, Dermaptera, Grylloblattodea* and *Phasmodea,* which are definitely more primitive than *Orthoptera;* this can in most cases be proved by palaeontological evidence and by comparative morphology. Therefore, it is significant that in *Proscopiidae* (in the species studied) the phallic complex is not fully bilaterally symmetrical. This is the only family in *Acridomorpha* with such a feature, which suggests that *Proscopiidae* is the most primitive family; here again, this could be a secondary development, but to decide this, it is necessary to study the postembryonic development thoroughly in the whole of *Proscopiidae* and *Eumasticidae.*

The number of instars in the *Acridomorpha* cannot supply a clue to interrelations, since it fluctuates in every group (see page 421), but there is nevertheless a hint that the evolutionary trend is toward a reduction of the number of instars. The subfamily *Truxalinae,* particularly in higher latitudes, is in general the most advanced; on average it has fewer instars than the other groups. This may, however, be a result of a shortened season of reproduction with longer days.

In the vermiform larva of every superfamily, family and subfamily all the features which characterise these taxa are rather obscured by the process of apolysis which is in progress even when the larva has not yet reached the surface of the soil. In the first instar all the characters are clear and can be judged by comparative study. Some of the gross characters, such as the shapes of the head, antennae, pronotum and legs, are rather suggestive. The head of a newly hatched vermiform larva in all superfamilies is subglobular or obtusely subconical. However, in many species of various groups it changes its shape rapidly between the vermiform larva and the first instar, whereas in others the change is gradual or does not occur at all. It could be concluded that the subglobular shape of the head is the most primitive.

The antenna is, in the vermiform larva, short, slightly flattened and ribbon-like, becoming filiform in the first instar. In most cases it remains filiform during the whole nymphal stage and in the imago. In some species, the antennae (fig. 17) change drastically at the first ecdysis into the shape which they preserve during all subsequent instars, including the imago, while in others they change only at the last ecdysis *(Cyathosternum).* It is considered that the filiform antennae are the most primitive. Reduction of the number of antennal segments is a progressive character. All the more primitive suborders of *Orthoptera* except *Tetrigoidea* have multi-segmented antennae. The very drastic reduction in the number of segments which occurs in *Lathiceridae,* however, may be considered as an adaptive character, *Lathiceridae* having the ability to bury themselves in the soil; they have very short antennae and grooves on the frons into which they can be retracted, probably to protect them from damage during burrowing. These characters are obviously best suited to the mode of life of these insects.

It cannot be decided by direct observation whether the fastigial furrow is a primitive or a progressive character, because of the difficulty of determining in the vermiform larva and even the first instar whether the line in question is indeed the furrow or whether it is an ecdysial cleavage line. It is certain, however, that if the fastigial furrow exists in the imago it is clearly detectable in the vermiform larva. Considering all the characters and their combinations in *Acridomorpha,* it will be justifiable to suppose that the presence of the fastigial furrow indicates primitiveness.

In all *Acridomorpha* the pronotum in the vermiform larva is a simple cylinder-lige structure. Sometimes it does not change during the whole of the nymphal stage or in the imago, whereas in other groups it changes its shape at the first ecdysis and remains almost the same in every subsequent instar and in the imago, as in *Porthetinae.* In others again the imago shape is acquired only at the last ecdysis *(Trigonopterygidae).* If we accept that the ontogeny to a certain degree reflects the phylogeny, it follows that the simple cylindrical or subcylindrical pronotum is the most primitive. However, it is possible that this character is purely an embryonic adaptation, and that it is the first instar, not the vermiform larva, that reflects the phylogeny. In most groups of *Acridomorpha,* in the first and subsequent instars the pronotum is compressed laterally, acquiring the imaginal shape at the last ecdysis.

One of the characters most frequently used in higher taxa is the comparative length of the basal lobes of the hind femur. In seven families of *Acridomorpha,* in the imago, the lower lobe is longer, in four it is shorter and in three the lobes are of equal length, or, as in the heterogeneous family *Eumastacidae,* they can be in any one of these three categories. In the vermiform larva the lobes are often indistinguishable. In the first instar, in all except one of the families, the lower lobe is longer than the upper; in some (table 3) it remains longer in the imago, but in others it becomes shorter with every ecdysis and is significantly shorter in the imago. This suggests that the longer lower lobe may be considered more primitive.

Reviewing all the external characters used in taxonomy for the families and subfamilies of *Acridomorpha,* it can be noted that all of them are present already in the vermiform larva. However, some of those that occur in the early instars either undergo reduction as development proceeds and disappear in the imago, or reverse their trends, like the lower basal lobe of the hind femur becoming shorter than the upper in *Acridinae* and *Truxalinae*.

In the family *Acrididae* some of the characters of the subfamilies are not apparent up to the second or third instar; an example is the rectangular shape of the mesosternal lobes in *Cyrtacanthacridinae*. But in *Truxalinae* the presence of the stridulatory serration on the inner side of the hind femur can be detected as early as the vermiform larva.

Brunner's organ is absent in the nymphal stage and in the imago in the family *Proscopiidae* only. In other families *(Pneumoridae)*, it can be absent or very reduced in the genera which have almost lost the ability to jump. Thus it is possible that in *Proscopiidae*, which are sluggish and jump only a short distance, the absence of Brunner's organ is not a primitive character of the family but is due to degeneration associated with reduced jumping ability. In six families of *Acridomorpha* the tympanal organ is normally present. It is probably a progressive character. In eight families it is absent, but in some of them this is probably due to secondary reduction; in the family *Lentulidae* it is possibly so, because in *Lentula* there is a suspicious thinning of the integument on the first abdominal tergite in the place where the tympanum is usually located. The tympanum is primarily absent in the superfamilies *Eumastacoidea* and *Trigonopterygoidea* and its absence probably indicates the primitiveness of these superfamilies.

The conclusion can be drawn that although in *Acridomorpha* recapitulation in the post-embryonic ontogeny cannot be definitely proved, there are several points which indicate that some characters are more primitive than others.

According to the information outlined above, the superfamily *Eumastacoidea* is the most primitive of all *Acridomorpha*. Comparison of the phallic complex of the imago confirms this view. It is so different from that of other superfamilies that the homology of the parts is doubtful. The general plan of the phallic complex in this superfamily is rather simple, comprising an endophallic sac and ectophallic structures, but while the functional parts are similar to this in the superfamily *Acridoidea* the origin of the parts is possibly quite different (Dirsh, 1956). This places the superfamily *Eumastacoidea* in a position rather isolated from other *Acridomorpha;* it is possible that it originated from some ancestral stock different from the stock of the other superfamilies, and also that the family *Eumastacidae*, which is highly heterogeneous, is polyphyletic in its origin as well.

The affinity of the superfamily *Trigonopterygoidea* is still rather obscure, but the structure of the phallic complex, despite its inverted position, approaches that of the *Pneumoroidea.* A poorly developed cingulum and a shield-like epiphallus are common characters for these two superfamilies which, however, differ in the arrangement of the other parts of the complex. If this superfamily was derived from the same stock as the *Acridoidea,* it must have branched off at a very early stage.

The phallic complex of the superfamily *Pneumoroidea,* in combination with other morphological characters, suggests affinity with the *Acridoidea,* but the complex is simpler, with simple endophallus, poorly sclerotized ectophallus and shield-like epiphallus. The interrelationship between the families of *Pneumoroidea* is difficult to define, as they are very divergent and all of them — *Tanaoceridae, Xyronotidae* and *Pneumoridae* — are probably relics of more ancient groups. The phallic complex and sound-producing mechanism unite them together and separate them from the other superfamilies.

The most advanced superfamily is *Acridoidea.* Most of its families have a tympanal organ and all of them possess a strongly sclerotized and well differentiated endophallus and ectophallus. Most of them have a tegmino-femoral stridulatory mechanism, or some other mechanism serving the same purpose. All these characters indicate a more advanced evolutionary stage of development.

The interrelations of the families of *Acridoidea* may be considered as follows:

The *Charilaidae* and *Pamphagidae* have common characters; the lower basal lobe of the hind femur is longer than the upper one (except in one genus in *Charilaidae),* the fastigial furrow is present, and the epiphallus is shield-like. All these characters are to be regarded as primitive, and the last two are also found in *Trigonopterygoidea* and *Pneumoroidea* which are probably, as has been suggested above, more primitive than *Acridoidea.* This indicates that the *Charilaidae* and *Pamphagidae* are the most primitive of *Acridoidea;* the *Charilaidae* are probably the most primitive of all.

The *Pyrgomorphidae,* however, also have the lower basal lobe of the hind femur longer than the upper and a fastigial furrow, but the phallic complex, including the epiphallus, is very different. This suggests that the family may not have arisen from the same branch of the common stock of *Acridoidea* as *Charilaidae* and *Pamphagidae.*

The family *Lathiceridae* is difficult to connect with the other families. Its species have the lower basal lobe of the hind femur longer than the upper and also have the fastigial furrow. In the phallic complex the apical and basal valves of the penis are disconnected, which suggests remote affinity with *Charilaidae,* the capsule-like cingulum suggests a connection with *Pyrgomorphidae* and the epiphallus, which is bridge-shaped, with oval sclerites, suggests affinity with *Acrididae.* It is possible that *Lathiceridae* separated very early from the ancestral stock of *Acridoidea* and preserved the primitive characters, namely the lower basal lobe of the hind femur being longer than the upper, and the fastigial furrow; at the same time the *Lathiceridae* may have acquired more advanced characters of the phallic complex, notably the bridge-shaped epipallus with the oval sclerites present which appears in *Acrididae.*

The family *Ommexechidae* is also most difficult to place in the phylogenetic system. It is distinct in its phallic complex, but the basal lobes of the hind femur are of equal length and the fastigial furrow, though not very clear, is present. Probably this family is one of the early branches of the *Acridoidea* stock, arising relatively near to *Pyrgomorphidae* but perhaps a little later.

The family *Pauliniidae* has some advanced external characters — the lower basal lobe of the hind femur is shorter than the upper and the fastigial furrow is absent — and these characters connect *Pauliniidae* and *Acrididae.* The divided valves of the penis, however, suggest affinity with the more primitive families, and the epiphallus has certain similarities with *Ommexechidae.* Possibly *Pauliniidae* originated from the earlier branch of the *Acridoidea* stock and being confined to an aquatic habitat preserved and developed the peculiarities mentioned.

The family *Lentulidae* is a degenerated branch of the *Acridoidea.* The wings and tympanal organ have been lost and the general appearance is nymph-like. Possibly the whole family is neotenic. The phallic complex contains certain primitive characters — a half capsule-like cingulum, undivided valves of the penis and a very simple epiphallus — but the epiphallus is bridge-shaped and oval sclerites are present. These characters suggest affinity with *Pyrgomorphidae* on the one hand and with *Acrididae* on the other. Probably they were branched from *Acridoidea* stock comparatively late.

The family *Acrididae* is one of the most advanced families of *Acridoidea.* Most of its members possess a tympanal organ and some form of sound-producing mechanism, and the lack of them in some cases is probably a result of secondary reduction. The phallic complex is simple, with valves divided or flexured, the epiphallus predominantly bridge-shaped and oval sclerites present. A particularly significant point is that the general structure of the phallic complex is rather uniform throughout the family, indicating that the family is recent and that divergence in the structure has not progressed very far. The subfamilies *Acridinae* and *Truxalinae* in which the phallic complex is so simiiar that sometimes it cannot be used even as a generic character, are probably the most recent.

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